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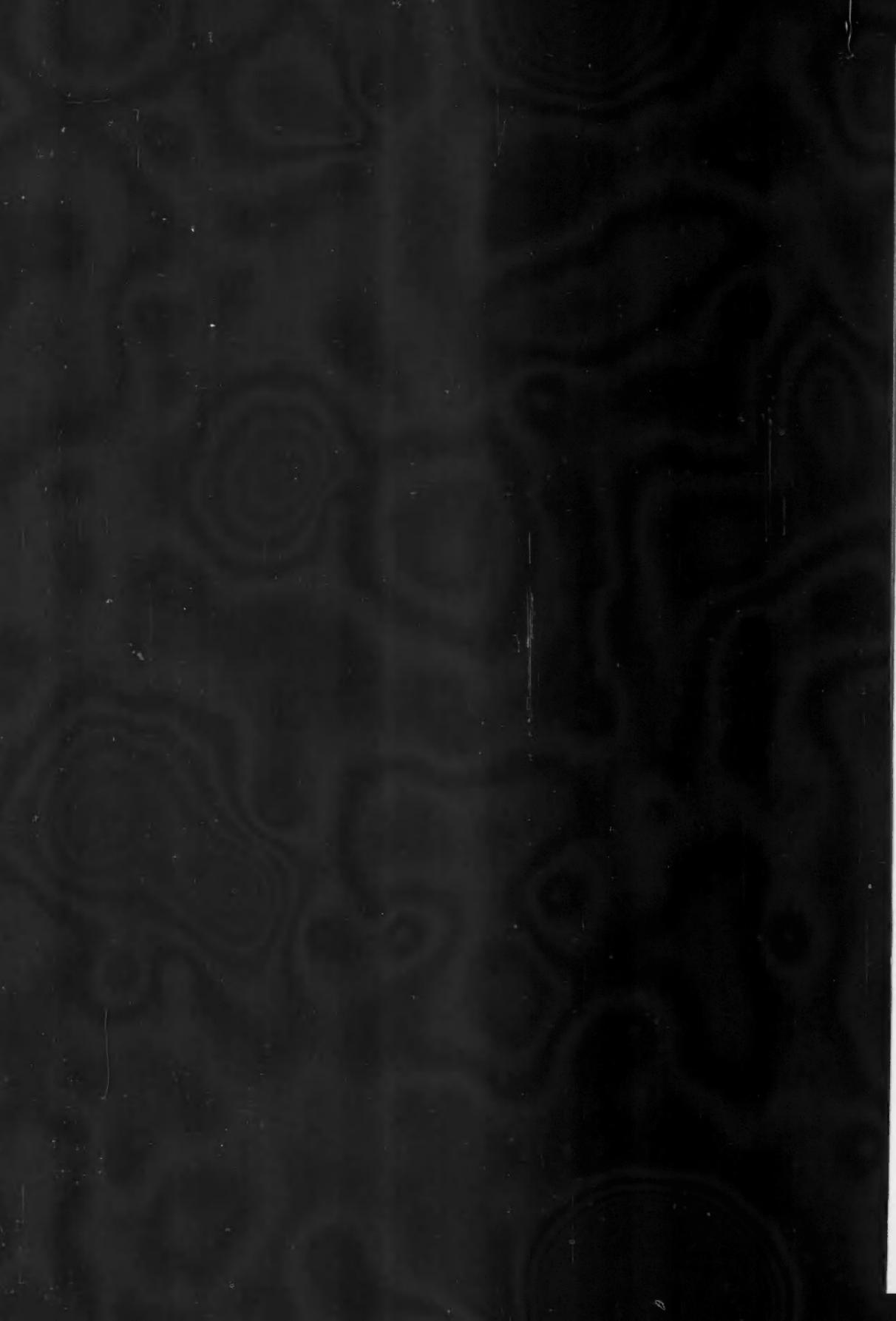
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REDUCTION OF *TRIAENOPHORUS* INFESTATION IN WHITEFISH BY DEPLETION OF THE CISCO POPULATION¹

BY RICHARD B. MILLER²

Abstract

In 1940 the catch of cisco in Lesser Slave Lake increased to over a million and a half pounds; it has remained at this high level for eight years, in the last two of which the catch has exceeded three million pounds. The age composition of the catch has decreased from nearly 80% six-year-olds or older to nearly 80% two-year-olds. During the period 1944-1947 the number of *Trienophorus* cysts in the whitefish has decreased from 265 per 100 fish (102.7 per 100 lb.) to 26 per 100 fish (6.8 per 100 lb.). This paper presents the evidence that indicates that this reduction of infestation in the whitefish has been a result of the depleted cisco population.

Introduction

The tapeworm, *Trienophorus crassus* Forel, lives as an adult in the intestine of the northern pike, *Esox lucius* L. The first larval stage (procercoid) is passed in the copepod, *Cyclops bicuspidatus* Claus, and the second larval stage (plerocercoid) is passed as a cyst in the flesh of, principally, the coregonine fishes. The presence of these cysts in the flesh of whitefish seriously interferes with the marketability of the fish; some means of reducing this infestation is highly desirable.

The study of the details of the parasite's life history was begun in Alberta lakes in 1939 in the hope that their complete elucidation would point the way to control measures. This study of the life history details has been more or less completed and the results published (2, 3, 5). The various possibilities of reducing or eliminating *Trienophorus* infestation, made apparent by a knowledge of the life history, have been outlined in an Alberta Government publication (4).

One of the methods suggested in this publication (4), an attack on the early free-swimming larval stage, has been attempted (Miller and Watkins, 7); in this experiment an unsuccessful attempt was made to acidify a lake in order to kill the coracidia of the parasite. Further experiments on this possibility of control are still being conducted. The present paper reports

¹ Manuscript received January 2, 1948.

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the results of another, long-term method of attack. In this method the reduction of infestation is sought through depletion of the tullibee* (cisco) population in Lesser Slave Lake.

The publication (4), referred to above, outlined the main arguments for regarding the tullibee as the principal second intermediate host. These arguments are here recapitulated:—

1. In any lake where infestation of whitefish and tullibee occurs, the tullibee are always the more heavily infested.

2. In at least six Alberta lakes there are whitefish but no tullibee; northern pike and *Cyclops bicuspidatus* are present. In all of these lakes the whitefish are free of *Triaenophorus* infestation. It would appear that the tullibee are necessary in the life cycle of the parasite.

3. Miller (6) has shown that parasitized whitefish grow more slowly than clean whitefish, whereas parasitized tullibee grow at a rate not significantly slower than clean tullibee. The association of host and parasite that produces the lesser disturbance is surely the more natural.

These three pieces of evidence suggest strongly that if the tullibee could be eliminated from infested lakes the whitefish would become free of infestation. Complete elimination of a fish in a large lake is practically an impossibility. That complete elimination of tullibee to accomplish parasite reduction is not necessary may be seen by examining the data in Table III. This table shows the degree of infestation of each age group of tullibee in Lesser Slave Lake; it is apparent that tullibee do not become heavily infested until they are four-year-olds. To effect an appreciable reduction in parasites, then, it is only necessary to remove tullibee four years old and older. Accordingly, in 1940, the Provincial Fisheries Branch, faced with a large demand for mink feed and understanding the chance of parasite reduction, removed virtually all limitations to the taking of tullibee in Lesser Slave Lake.

The Depletion of the Tullibee

For the five year period ending in 1939 the average annual catch of tullibee in Lesser Slave Lake was 63,000 lb. Catches since then are shown in Table I.

TABLE I
THE ANNUAL* CATCH OF TULLIBEE IN LESSER SLAVE
LAKE SINCE 1940 (LB.)

1940-41 - 1,504,900	1944-45 - 1,349,020
1941-42 - 1,993,900	1945-46 - 1,491,981
1942-43 - 1,770,600	1946-47 - 3,556,587
1943-44 - 1,475,900	1947-48 - Over four million

* The fishing year does not correspond to the calendar year but comprises the winter and succeeding summer.

* The ciscos in western Canada are usually referred to as tullibee, although species other than tullibee, sensu strictu, commonly occur.

The enormously increased catches of the past eight years and particularly of the last two years have had a profound effect on the tullibee population. This effect may be traced in the changing age composition of the catches as shown in samples taken since 1941. There has been no change in the commercial gear used to catch the tullibee throughout this period. The gear used is gill net of $2\frac{3}{4}$ in. mesh, stretched measure. All samples were taken with this gear. The age composition of these samples is shown in Table II. Unfortunately, no data are available for 1946. Altogether the ages of 1348 tullibee have been determined.

TABLE II
THE AGE COMPOSITION OF THE SAMPLE CATCHES OF TULLIBEE
FROM LESSER SLAVE LAKE, 1941-1947

Year	Number of fish in sample	Ages and percentage of each age in sample								
		1	2	3	4	5	6	7	8	9
1941	118	0	0	2.6	5.8	12.7	42.3	26.3	10.2	0
1942	85	0	0	4.7	1.2	16.5	65.9	11.7	0	0
1943	99	0	0	6	9	27	38	17	2	0
1944	545	2.3	5.8	4.4	8.8	17.4	27	27.5	6.4	0.4
1945	100	0	18	7	12	16	17	24	5	1
1947	401	4.7	78.5	15	1	0.7	0.2	0	0	0

At the time when heavy fishing began in Lesser Slave Lake the catch consisted of about 80% six-year-old or older fish. Slightly more young fish showed up in the samples of 1942. By 1943 about half the catch (as represented by the sample) was less than six years old; in 1944 and 1945 one- and two-year-old fish appeared in the samples. In 1947, 78.5% of the sample was of two-year-old fish and only 16.9% was older than two.

These figures suggest a great reduction in the tullibee population. The effect that this has had on the quantity of *Trienophorus* cysts in the tullibee is discussed in the next section.

The Change in the Infestation of the Tullibee

At the beginning of the period of increased tullibee catches close to 100% of these fish were infested with cysts of *Trienophorus*. More or less casual checks from time to time showed no appreciable change in the next few years. In 1944 a thorough measurement of the infestation of each age group of tullibee was made; further careful examinations were made in 1945 and 1947. The results of these are shown in Table III.

With the removal of the older tullibee through heavy fishing there has been a spectacular reduction in total percentage infestation from close to 100 to about 11%; the average infestation has decreased from 890 cysts per 100 fish (all ages) to 15.4.

TABLE III

THE INFESTATION OF TULLIBEE OF LESSER SLAVE LAKE WITH CYSTS OF *Triadenophorus crassus*, 1944-1947. THE FIGURES IN THE TABLE REPRESENT CYSTS PER HUNDRED FISH

Date	Number of fish	Age of fish									Av. all ages	Fish infested, %
		1	2	3	4	5	6	7	8	9		
Jan.-Feb. 1944	332	—	—	82	760	1078	910	1012	437	—	890	93
May-Oct. 1944	213	0	15.6	200	280	992	1225	820	1121	633	754	76
Jan.-Feb. 1945	100	—	5.6	28.5	733	770	880	835	540	100	591	75
Oct. 1947	100	0	8.4	20	—	800	1200	—	—	—	37	10
Nov. 1947	201	0	6.6	40.9	0	300	—	—	—	—	15.4	11.4

Carlander (1), studying tullibee in Lake of the Woods, Minn., mentions a decrease in infestation with *Triadenophorus*. He also finds a shift to the younger age groups of tullibee associated with heavier fishing and it is possible that the parasite reduction is related to this change.

If the argument given in the introduction is correct, i.e., if the tullibee is the principal second intermediate host of *Triadenophorus crassus*, then the whitefish in Lesser Slave Lake should show decreased infestation. In the following section data on whitefish infestation are presented.

Triadenophorus Cysts in Whitefish

The first investigation of these cysts in whitefish of Lesser Slave Lake was made in the summer of 1940 when 123 whitefish were cut up in a search for the parasites. Thirty-five per cent of these fish were infested at a rate of 52.5 cysts per 100 lb. and 131 cysts per 100 fish. In 1941 a sample of 81 whitefish was found to be 24.7% infested. No cyst count was made. Fishermen reported similar high infestations during the seasons of 1942 and 1943.

Large samples of whitefish were carefully cut up to make cysts counts in 1944, 1945, and 1947. Scales were taken from each whitefish and from these the ages of the fish have been determined. The data are shown in Table IV.

There has been a very considerable reduction of infestation in the whitefish. The average of cysts per 100 fish has decreased from 265 to 26, the average of cysts per 100 lb. from 102.7 to 10.5, and the percentage of fish infested from 30.8 to 6.8. That this reduction is not just random fluctuation is shown by the figures for cysts per 100 fish of each age group. Significant numbers of fish were examined in the three- to seven-year-old age groups. It can scarcely be chance that there is a consistent reduction of infestation in each of these age groups from 1944-1947.

TABLE IV
THE INFESTATION OF WHITEFISH OF LESSER SLAVE LAKE WITH CYSTS OF *Triadenophorus crassus*, 1944-47.
FIGURES IN PARENTHESES GIVE NUMBER OF FISH EXAMINED

Date	Number of fish*	Age and cysts per 100 fish							Av. cysts per 100 fish	Av. cysts per 100 lb.	Fish infested, %
		3	4	5	6	7	8	9			
Sept. 1944	490	240 (51)	65.5 (203)	94.3 (107)	260 (39)	882 (34)	1556 (38)	453 (8)	265	102.7	30.8
Oct. 1945	500	0 (2)	94 (104)	63 (186)	189 (121)	408 (60)	1054 (22)	40 (2)	185	54.7	17.4
Oct. and Nov. 1947	601	0.7 (139)	6.5 (355)	41 (49)	35 (23)	328 (14)	345 (9)	357 (7)	26	10.5	6.8

* The total number of fish examined does not agree exactly with the total of the figures in parentheses as a few fish older than nine and younger than three have been omitted.

Discussion and Conclusions

The data presented in this paper show that when the tullibee population consists largely of young fish the infestation with *Triaenophorus* cysts becomes very small. The data also show that, since the tullibee is the principal second intermediate host of the parasite, the small parasite population in tullibee results in a small parasite population in the whitefish as well. The record of the age composition of tullibee populations in Lesser Slave Lake since 1941 suggests that the present preponderance of young fish has resulted from overfishing. It follows, therefore, that overfishing of the tullibee will produce a decreased infestation of whitefish with *Triaenophorus* cysts. The author feels that the evidence for this conclusion is strong enough to warrant advising administrators who have a *Triaenophorus* problem to try overfishing of tullibee as a cure. The tullibee gear may take some of the young of other species of fish but the damage done in this way is not commensurate with the achievement of significantly reduced infestation.

Acknowledgments

This work could not have been done without the whole-hearted cooperation of the Alberta provincial administration. I am greatly indebted to the Honorable N. E. Tanner, Minister of Lands and Mines, and Mr. E. S. Huestis, Fish and Game Commissioner, for giving their support to this work; and I owe special thanks to Mr. H. B. Watkins, Superintendent of Fisheries. The large amount of work involved in measuring, weighing, and counting the cysts in nearly 1600 whitefish and 1300 tullibee was done by the fisheries field officers under Mr. Watkins' direction.

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OBSERVATIONS ON *LEUCOCYTOZOON* INFECTIONS IN BIRDS RECEIVING PALUDRINE, ATEBRIN, AND SULPHAMERAZINE¹

A. MURRAY FALLIS²

Abstract

Paludrine, atebrin, and sulphamerazine neither prevented nor cured infections with *Leucocytozoon simondi* in ducklings, nor did they have any noticeable effect on the course of the infections. Paludrine failed to cure an established infection of *Leucocytozoon sakkaroffi* in a crow. The extensive 'tissue stages' of these parasites probably explain the negative results.

The extensive tests on the use of atebrin and paludrine for the prevention and cure of malaria (Fairley (5, 6), Curd, Davey, and Rose (2-4)) have supplied further data on the biology of the parasites that cause this disease. It was considered of interest therefore to test the effects of these drugs on the parasites in the related genus *Leucocytozoon*.

O'Roke (8) tested the efficacy of quinine sulphate and dihydrochloride and Plasmochin on the gametocytes of *Leucocytozoon simondi* in ducks but found them ineffective. Coatney and West (1) administered atebrin to a great horned owl and a juvenile red-tailed hawk that had heavy infections of a spindle type of *Leucocytozoon*. They concluded that the drug has some effect inasmuch as it produced morphological changes in the form of clear vacuoles in the parasites and the host cells.

In the present experiments the prophylactic and curative value of paludrine and atebrin on *L. simondi* was tested as follows: 19 10-day-old ducklings were left in the open to be bitten by black flies. Paludrine and atebrin were given orally to eight of the ducklings 12 hr. after the first exposure to black flies and daily thereafter for 15 days. Four of these ducklings received 1 mgm. paludrine per day and four received 2 mgm. atebrin. The other ducks served as controls and a number in this group showed infection in the blood 11 to 12 days after their first exposure to black flies. Three of these ducklings were each given 2 mgm. atebrin t.i.d. for four days following the appearance of infection. Four of the ducklings received 1 mgm. paludrine t.i.d. for four days following the appearance of parasites in the blood. This left four birds in the entire group as controls that received no treatment. Blood smears, which were made daily from each bird, were stained with Giemsa and examined for parasites. The date on which the first parasites were observed in the blood as well as the number in a count of one minute on the smear were noted (Table I).

It will be observed from the data in this table that neither paludrine nor atebrin in the above dosages prevented or cured infection with *L. simondi*.

¹ Manuscript received December 10, 1947.

Contribution from the Department of Parasitology, Ontario Research Foundation, Toronto, Ont.

² Director of Parasitology.

TABLE I
TREATMENT WITH PALUDRINE AND ATEBRIN

Duck No.	Treatment	Date gametocytes observed	Date of peak infection	Number parasites in 1 min. count on smear at peak of infection
10	1 Mgm. paludrine	June 28	July 9	38
11		June 24	June 28	37
12	daily,	June 28	June 30	24
13	June 13 to 28	June 25	June 29	13
14	2 Mgm. atebatin	June 24	June 25	31 Died July 9
15		June 24	June 25	130 Died June 30
16	daily,	June 24	June 28	91 Died July 12
17	June 13 to 28	July 4	July 5	6
18		June 23	—	61 Died June 23
19	Controls	June 24	June 28	147
20		June 25	June 26	36
21		June 29	June 30	56
22	2 Mgm. atebatin	June 25	June 30	39
23	t.i.d.,	June 25	June 27	146
24	June 25 to 29	June 24	June 26	82
25	1 Mgm. paludrine t.i.d.	June 25	June 28	34
26		June 24	June 29	114 Died July 10
27	June 25 to 29	June 25	June 29	74
28		June 24	June 29	91

in ducks. There was no marked difference in the level of infection in the blood in the treated vs. the control birds. No morphological changes were noted in the parasites that might have been caused by the drugs. Fairley (6) found that although paludrine did not destroy gametocytes of *Plasmodium* in man it prevented their further development in mosquitoes that had fed on gametocyte carriers receiving the drug. No such effect was observed in the present study as the parasites developed to oökinetes in the black flies that fed on a bird receiving the drug.

In a second experiment three ducklings that were two weeks old were each given orally 50 mgm. sulphamerazine daily for over three weeks, beginning on the date on which they were first exposed to black flies. Two ducklings of the same age were kept as controls. Some of the results of this experiment are shown in Table II. It will be observed that the drug did not prevent infection becoming established nor did it have any apparent effect on the level of infection reached in the treated vs. the control birds.

A single crow, showing a high gametocyte level of *L. sakharoffi* and evidence of leg paralysis thought to be due to the infection, was given 2 mgm. paludrine four times a day for four days but it failed to recover.

TABLE II
TREATMENT WITH SULPHAMERAZINE

Duck No.	Treatment	Date gametocytes observed	Date of peak infection	Number of parasites in 1 min. count on smear at peak of infection
33	50 Mgm.	July 16	July 26	23
34	sulphamerazine,	July 13	July 18	44
35	July 4 to 31	July 16	July 19	57
36	Controls	July 16	July 20	41
37		July 12	July 19	151

Discussion

It appears from these experiments that the drugs paludrine, atebrin, and sulphamerazine, in the dosages used, have no value in preventing infection with *Leucocytozoon simondi*. Neither did the two former drugs cure infections that were established. The dosages of paludrine and atebrin on a weight basis are slightly greater than those that are used successfully on man. The results with atebrin are perhaps not comparable with those of Coatney and West (1) who administered large quantities of the drug. The sulphamerazine dosage was similar to that which has been used successfully by Swales (9) for coccidia in chickens. It may be argued that the drugs are ineffective against the sexual forms of the parasite. However, these must arise from the stages in the tissues. Unless the 'tissue stages' that produce gametocytes do so exclusively, and have a long life, this is not the sole explanation as otherwise the infections would not persist in the birds without more or less continuous asexual development. It seems more probable that the drugs were not effective against the 'tissue stages' (Huff (7), Wingstrand (10)) rather than that the dosages were inadequate. Such an explanation would support the view that the preventive and curative effects of these drugs on malaria are related to the nature and extent of the 'tissue stages'. It will be of interest, for these reasons, to explore more fully the relationships between schizogony and gametogony in *Leucocytozoon* and to obtain a more complete understanding of the sequence of asexual stages.

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I wish to thank Dr. H. B. Speakman, Director, Ontario Research Foundation, for permission to carry out these experiments and for his kindly advice. I am grateful to Mr. John Pearson for assistance with the experiments and I am indebted to Imperial Chemical Industries for supplying the paludrine.

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ON THE CHEMOTHERAPY OF CAECAL COCCIDIOSIS
(*Eimeria tenella*) OF CHICKENS

VI. A NOTE ON THE METABOLISM OF CAECAL EPITHELIUM,
NORMAL AND PARASITIZED¹

BY H. B. COLLIER² AND W. E. SWALES³

Abstract

The respiration and anaerobic glycolysis of caecal tissue of chickens were measured; the values obtained were similar to the corresponding values for rat intestine.

Infection of the caecal mucosa with coccidia (*Eimeria tenella*) produced no significant change in metabolic rate. Sulphamerazine, which is coccidiostatic *in vivo*, did not affect the metabolism of tissue strips.

Introduction

Work on the control of caecal coccidiosis of chicks has demonstrated that the sulphapyrimidine drugs are strongly coccidiostatic and that they exert their strongest inhibitory effect upon the merozoites (Swales (12), Ripsom and Herrick (10)). Recently it has been shown that the schizonts containing second generation merozoites are largely destroyed by sulphamethazine (Farr and Wehr (5)). Knowledge of the relative metabolic activity of the normal host tissues and of the tissues at various stages in the parasite's life cycle would be of great value in work designed to clarify the mode of action of coccidiostatic drugs; it might also lead to a means of testing chemicals *in vitro* for coccidiostatic properties. The work herein reported was an attempt to find differences in metabolic activity between normal caecum and caecal tissue parasitized by various stages of *Eimeria tenella*.

Christophers and Fulton (1) initiated the biochemical study of blood in which malaria parasites, *Plasmodium* spp., were established. More recent studies of malarial blood have been carried out by McKee *et al.* (9), Evans (4), and Hellerman *et al.* (6). They were able to demonstrate an increased metabolic activity in parasitized erythrocytes, and under some conditions the metabolism of the parasites was inhibited by antimalarial drugs such as quinine and quinacrine.

Experimental

Methods

Chicks of various breeds, from 7 to 10 weeks of age, were used. To obtain normal tissue the chicks were taken from batteries in a room kept free of coccidia, killed by decapitation, and the caeca were opened, rinsed in isotonic

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saline at 40° C., and rapidly prepared as described below. Parasitized caeca were similarly obtained from chicks from the same group that had been dosed per os with 100,000 sporulated oocysts of *E. tenella* and killed at appropriate times thereafter.

The metabolic activity of caecal tissue was measured by methods similar to those employed in a study of tissues of the mammalian alimentary tract by Dickens and Weil-Malherbe (2) and by Lutwak-Mann (8). Since mucosa disintegrates rapidly when separated from the muscular layers, we used strips of the whole wall of the caecum cut to about 2 to 3 by 30 mm. in size and weighing 50 to 100 mgm. The tissue was blotted with filter paper, the wet weight was measured, and it was then used immediately for metabolic studies. The ratio of wet weight to dry weight was determined upon similarly treated strips from the same organ, dried at 110° C. for two hours.

Oxygen uptake and anaerobic glycolysis were studied by standard manometric methods (Dixon (3)), with Summerson differential manometers attached to flasks of about 15 ml. capacity. All runs were made in replicate at 41° C. for two hours, with shaking at a rate of 120 oscillations per minute and 4 cm. amplitude. In experiments with sulphamerazine the sodium salt was added in amounts sufficient to give a concentration of 0.001 M in the medium.

Tissue Thickness and Dry Weight

The mean thickness of whole caecal wall was 1.00 ± 0.09 mm. (eight determinations).* The dry weight was found to be $17.6 \pm 0.2\%$ of the wet weight (26 determinations). Invasion of the mucosa by parasites resulted in congestion and swelling of the caecal wall (up to 2.0 mm.), but did not change the percentage of dry weight.

In a few experiments the mucosa stripped from the muscular wall was used. The thickness of the mucosa alone was 0.3 to 0.5 mm., and the dry weight averaged $16.2 \pm 0.4\%$ of the wet weight.

Oxygen Uptake

The limiting thickness of tissue for maximum oxygen uptake has been estimated as 0.5 mm. (3), and the thickness of the caecal wall exceeded this limit. Preliminary experiments indicated, however, that respiration in air was only 25% less than in pure oxygen; and as the greatest metabolic activity resided in the mucosa it was believed that the results were not greatly affected by the thickness of the tissue strips.

All subsequent respiration determinations were run in pure oxygen. The rate of oxygen uptake did not remain constant over the two hour period, but fell off slightly from the linear, as indicated in the result of a typical experiment:—

40 min.....	— 110 μ l. oxygen
80 min.....	— 210 μ l. oxygen
120 min.....	— 296 μ l. oxygen

* All averages are reported as mean values \pm the standard error of the mean.

The Q_{O_2} values were calculated from oxygen uptake in the first 60 min.; and a summary of 14 determinations (five birds) gave a mean Q_{O_2} of -7.35 ± 0.45 . Results with parasitized birds are summarized in Table I, from which it is evident that the presence of parasites did not increase the rate of oxygen consumption. (In one experiment upon normal mucosa stripped from the muscular wall, the values obtained were: -9.4 , -9.8 , -10.3 .)

TABLE I
RESPIRATION OF NORMAL AND PARASITIZED CHICK CAECUM

Strips of whole caecum in 2.0 ml. of Krebs-Eggleson (7) phosphate saline, pH 7.4, containing 0.2% glucose. Gas phase oxygen, potassium hydroxide-filter paper in center well; 60 min. at $41^\circ C$.

Days after infection	Stage of parasite development	Condition of mucosa	Q_{O_2} (replicates)
0	—	Normal	-7.35 ± 0.45
1	First stage schizonts	—	-7.0 , -7.2
3	Developing schizonts	—	-6.8 , -6.8
4	First generation merozoites	Slight haemorrhage	-5.4 , -7.8
5	Second generation merozoites	Acute haemorrhage, congestion	-4.6 , -4.7

A concentration of 0.001 M sulphamerazine in the medium did not affect the respiration of either normal or parasitized tissue.

Anaerobic Glycolysis

Carbon dioxide production plotted against time gave a rate that was virtually constant for the two hour period or that fell off very slightly. The carbon dioxide production in the first 60 min. was used for calculating the values of $Q_G^{N_2}$.

The values for anaerobic glycolysis in whole caecum, normal and parasitized, are summarized in Table II. Sulphamerazine at 0.001 M concentration had no effect. A slight increase in glycolysis at the three day stage of parasite development is suggested. A few experiments upon mucosa alone also appear to indicate such an increase, although the difference is not statistically significant.*

Discussion

Caecal tissue, parasitized with *Eimeria tenella* at various stages of development, showed no increase in rate of respiration as compared with normal tissue; in fact, there was a slight decrease in respiratory activity in the acute stages of the disease, when the mucosa was congested and haemorrhagic.

* The difference in the mean values for normal and parasitized mucosa is 5.0 ± 2.1 . Hence the *t* value is 2.4, giving a probability of 0.05 to 0.10.

TABLE II

ANAEROBIC GLYCOLYSIS OF NORMAL AND PARASITIZED CHICK CAECUM

Strips of caecal tissue in 2.0 ml. of calcium-free Krebs-Henseleit Ringer-bicarbonate (3) containing 0.2% glucose. Gas phase 5% CO_2 + 95% N_2 ; 60 min. at 41° C.

Days after infection	Stage of parasite development	Condition of mucosa	$Q_G^{\text{N}_2}$ (replicates)
Whole wall	—	Normal	7.1, 7.6 7.2, 7.5
0		—	9.2, 9.8 8.0, 8.1, 8.2
3	Developing schizonts	—	9.2, 9.8 8.0, 8.1, 8.2
4	First generation merozoites	Marked haemorrhage	7.0, 7.6
7	Gametocyte	Very acute haemorrhage	6.3, 6.4
Mucosa alone	—	Normal	8.9, 10.0 9.5, 10.8, 12.9
0		No haemorrhage	11.5, 16.7, 17.9
3	Developing schizonts	—	—

Determination of anaerobic glycolysis revealed a slight but statistically insignificant increase at the third day after infection, especially when mucosa alone was used. A larger number of experiments would probably reveal a significant increase in the parasitized tissue.

When these results are compared with the findings obtained with blood parasitized with *Plasmodium*, it is evident that normal erythrocytes have a very low metabolic rate, which is notably increased by the presence of the parasites. In the case of intestinal tissue, on the other hand, the tissue itself possesses an active metabolism, and any additional activity due to the parasites is scarcely measurable.

Sulphamerazine is a strongly coccidiostatic drug, and might be supposed to inhibit the metabolism of the coccidia; but since the additional activity due to the parasites was not measurable, no effect of the drug could be observed. Furthermore, the low concentration of sulphamerazine in the medium may not penetrate to the parasites. If it were possible to measure a significant increase in glycolysis, a better method of investigating the effect of the drug would be to administer it to the chicks by mouth, in therapeutic doses, and then to measure the metabolic activity of caecal tissue after a suitable interval. The limited time available for this project precluded the carrying out of such experiments.

The values obtained for metabolism of chick caecal tissue were of the same order of magnitude as those observed with mammalian gastrointestinal tissue, as put forth in Table III. It may be estimated from our data that about two-thirds of the metabolic activity of the caecal tissue resides in the mucosa, although it occupies less than one-half of the total thickness.

TABLE III
COMPARISON OF METABOLIC ACTIVITY OF CHICK CAECUM AND
MAMMALIAN GASTROINTESTINAL TISSUE

Tissue	Q_{O_2}	Q_G^{N2}	Author
Chick caecum Whole wall Mucosa	— 7.4 — 9.8	7.4 10.4	Collier and Swales
Rat jejunum* Whole wall Mucosa	— 7.8 — 11.3	8.1 12.6	Dickens and Weil- Malherbe (2)
Rat stomach† Whole wall Mucosa	—8 to —15 —10	11 6	Lutwak-Mann (8)

* Based upon the first 20 min. period.

† Estimated from the graphs (60 min. values).

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ACCESSORY TAILS IN FROG TADPOLES, THEIR EXPERIMENTAL PRODUCTION AND SIGNIFICANCE

II. SOME EXPERIMENTAL METHODS OF PRODUCING ACCESSORY TAILS IN FROG TADPOLES¹

BY DAVID J. McCALLION²

Abstract

Under certain conditions of injury to the tail of the tadpole of *Rana clamitans* accessory tails arise by regeneration. Methods of obtaining these conditions are outlined and the resultant accessory tails are described. Previous literature dealing with the mechanism that initiates the regenerative process in frog tadpoles is discussed and interpreted in the light of evidence gained in studies of accessory tail formation.

Introduction

Of the many problems involved in regeneration, one of the more significant is that of internal influence. There is a vast and often confusing or conflicting literature dealing with the causative influences of various structures on the regeneration of a part in almost all the major groups of animals. In some cases the problem has been adequately dealt with. In others the results are not so satisfactory.

The present paper is largely concerned with the relative influence of the nerve cord and the notochord on the regeneration of the tail of the frog tadpole. Does one, or both, or indeed either, of these structures initiate the regenerative process or induce the formation of a tail? If these structures influence tail regeneration, is such influence a contact principle, effective only when these structures are present at the cut surface, or a diffusion principle that becomes less effective with distance from the cut surface?

Experimental studies of growth and regeneration in very early stages of development in frog larvae (by Barfurth, Goldstein, Braus, Harrison, and others) seem to indicate that the central nervous system does not exercise any morphogenetic influence on the development or regeneration of embryos. Other investigators (Morgan and Davis (11), Wintrebert (15), and Goldfarb (6)) have attempted to show that the nerve cord has no influence on the regeneration of the tail in older tadpoles. In some respects their results were not entirely satisfactory.

The experiments of Morgan and Davis consisted in amputation of the distal one-third of the tail, together with the extirpation of a short length of the nerve cord, or notochord, or both. The muscle masses on either side were necessarily removed at the same time. Wintrebert's experiments were somewhat similar. A portion of the tail was amputated and the stump was

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cut in several ways in order to produce two branches, or three branches in which nerve cord, notochord, and aorta were separated or variously combined. The results of both these sets of experiments were quite varied and not always in agreement with those of later investigators. However, they were interpreted as indicating that regeneration of the tadpole tail is independent of the nerve cord but dependent upon the notochord.

It has been stated that the results of these experiments are not in agreement with those of later workers. Goldfarb (6) and others have shown that the tail of the frog tadpole is innervated from ganglia lying in the anterior half of the tail. There are no ganglia in the distal half of the tail. It is obvious, then, that mutilations of the tail, as described above, interfere very little with the innervation of the stump. More important, however, is the difficulty of separating the nerve cord from the notochord. They are very closely applied to each other and the muscle masses surrounding them are opaque. As a result of this difficulty, fragments of nerve cord (and notochord) are usually present in the isolated parts. These fragments are themselves capable of regeneration. Therefore, although these experiments have tested, in some measure, the value of the intact nerve cord, they do not test the value of regenerating fragments nor of peripheral fibers.

When Tornier (14) repeated the experiments of Morgan and Davis he got no regeneration at all. He attributed this to physiological inhibition of regeneration exerted by the overhanging muscle masses. Later, Avel (1) showed that this was merely mechanical obstruction of regeneration.

The writer also attempted to repeat these experiments. After unsuccessful attempts to separate the notochord and nerve cord without injury to either, the distal one-third of the tail was amputated and sufficient tissue to include both nerve cord and notochord was cut out for a distance of several mm. (Fig. 1a). In only one of 10 cases studied did the overhanging muscles



FIG. 1. A line drawing to show the nature of the injury to the tail (a) after the method of Morgan and Davis (see text), (b) after the method of Wintrebert (see text).

meet and fuse, and thus block regeneration of the notochord. In the other cases the notochord grew through the cut region and at least five millimeters beyond the amputation level. These observations are in agreement with those of Avel and contrary to those of Tornier. Regeneration of the nerve cord was irregular but it was carried along with the notochord. The one important observation was that the upper and lower masses of muscle and connective tissue showed a small amount of regeneration (about 2 mm.) although some distance from the cut ends of the nerve cord and notochord.

Similarly, when the tail stump was split into three parts (after Wintrebert, Fig. 1b) it was never certain that the nerve cord and notochord were cleanly

separated. In every case a new tail regenerated from the middle piece. In most cases the outer parts became more or less fused with the central part. In those few cases in which either the upper or lower part remained free, and therefore, distant from the notochord at least, these parts showed some regeneration but never produced tails.

Having shown that the tip of the tail was innervated from ganglia at more proximal levels, Goldfarb attempted to denervate the tail in several ways, especially by transection of the nerve cord at the base of the tail. This usually resulted in such extensive injury or mutilation that the animals died. In those that survived he was never sure of a denervated stump, but from what results he got, he thought that in all probability the central nervous system has no influence on tail regeneration in frog tadpoles. On the other hand, he had already satisfied himself that, in adult urodeles, the determining factor in the formation of a tail is the presence of the nerve cord at the cut surface.

More exact studies on the influence of the notochord in development and regeneration have been possible. It has been demonstrated by Politzer (12) and Risley (13) that notochordal tissue has some influence in inducing embryonic tail formation in urodeles. Kollmann (8) and Francescon (4) showed that, if in frog tadpoles the notochord was destroyed or partially destroyed, and therefore, prevented from regenerating, the tail did not regenerate. Morgan and Davis (11) also claimed that the presence of the regenerating notochord at the amputation surface was essential to tail regeneration. Wintrebert (15) was of the opinion that it is the reconstitution of the notochord as a supporting axis, as much as any influence it might have, that regulates tail regeneration.

Accessory tails resulting from natural and experimental injury have been frequently recorded in lizards, urodeles, and frog tadpoles. In an earlier paper by the writer (McCallion (9)) five cases of accessory tails in frog tadpoles arising from natural injury were described. Varying in degree of perfection, they have been produced in frog tadpoles by a number of investigators.

Harrison (7), using Born's method of grafting, obtained forked tails in *Rana palustris* tadpoles. He severed the tails from two young larvae and united the larvae in such a way that their tail stumps met with their axes at an angle of about 135°. Later the notochord of one member of the pair had regenerated ventrally into the ventral fin fold of the other. This notochordal growth was accompanied by muscle and blood vessels. At this time the animals were cut apart so that the principal larva had a forked tail. In this manner, Harrison obtained 10 instances of bifid tails, a few of which also had a forked nerve cord. These structures are not, in the sense of this discussion, accessory tails, but the tail of one animal grafted upon the tail of another. Even though the grafts took well, the two notochords never became united.

Barfurth (2) tried to obtain bifid tails in *Rana fusca* tadpoles by splitting the tail into upper and lower parts, but with slight success. He was successful in producing such structures by a double injury to the tail. A hot needle was thrust into the side of the tail followed by amputation just posterior to the first injury. Subsequent regeneration produced a tail from each of the two sites of injury. By a somewhat similar procedure Avel (1) obtained similar results with *Rana temporaria*. The side of the tail was pierced in such a manner as to remove a short piece of notochord, but leaving the tail end attached. A small tail regenerated from the site of injury, assumed the normal axis, and pushed the old tail aside.

Material and Methods

Young *Rana clamitans* tadpoles, collected from a pond near McMaster University, were used in these experiments. They were kept in the laboratory in large numbers with considerable success. Animals used in experiments were first anaesthetized in Chloretone solution (1 : 1000 water). The cuts were made as quickly as possible with a fragment of razor blade fixed to a glass handle. After operation the animals were placed in Ringer's solution for 24 hr., and transferred to tap water for six weeks or longer. After that time the tails of these animals were photographed and prepared for histological examination.

Experiments and Results

METHOD I

A simple method of obtaining accessory tails in frog tadpoles is by incomplete amputation. If the tail is incompletely amputated by a single incision, it is difficult to prevent the edges of the wound from healing together. To overcome this difficulty V-segments or long segments were cut out from the dorsal edge of the tail in some cases (Figs. 2a, 2b), and from the ventral edge in others (Figs. 2c, 2d). Sufficient tissue was removed to include the notochord and this was, in effect, the same as an incomplete amputation. Forty-two cases were studied.

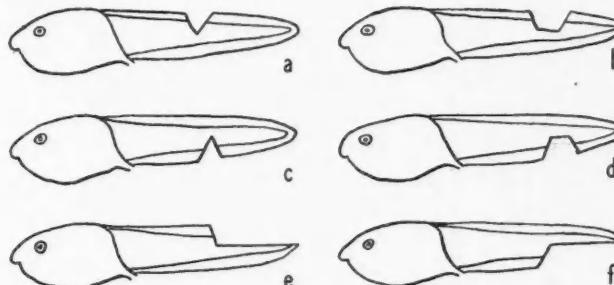


FIG. 2. Line drawings to show the amounts of tissue removed from the edge of the tail in Method I; a and c show V-segments, b and d long segments, e and f show the location and amount of tissue removed in Method II.

In a small number of cases the old tail end was torn away by the activity of the tadpoles. In these cases normal terminal regeneration followed. In a few instances the injury was not made sufficiently deep to include the notochord, and that portion of the tail that was removed was regenerated and a nearly normal structure resulted.

If the injury was made from the dorsal edge of the tail, and in such a way that the notochord was severed, regenerative growth proceeded from both surfaces of the cut. When the injury was sustained near the tip of the tail the posteriorly directed regenerate became an accessory tail (Figs. 3, 4, 5). It was more or less complete, lacking only a ventral fin fold. This structure possessed nerve cord and notochord accompanied by some muscle fibers. The caudal vessels, if present, were very irregular.

The nature of the anteriorly directed regenerate depended upon the location of the injury. Morgan (10) observed that if a cut was made into the dorsal edge of the tail near its base, regeneration from the anterior surface of the wound was slight but a heteromorphic tail arose from the posterior surface. It was noted in these experiments that if the injury was made in the middle regions of the tail growth from the opposing surfaces of the wound was nearly equal in rate and amount and the regenerates overlapped (Fig. 6). At the tip of the tail regeneration from the anterior surface was greater and an accessory tail resulted (Fig. 4).

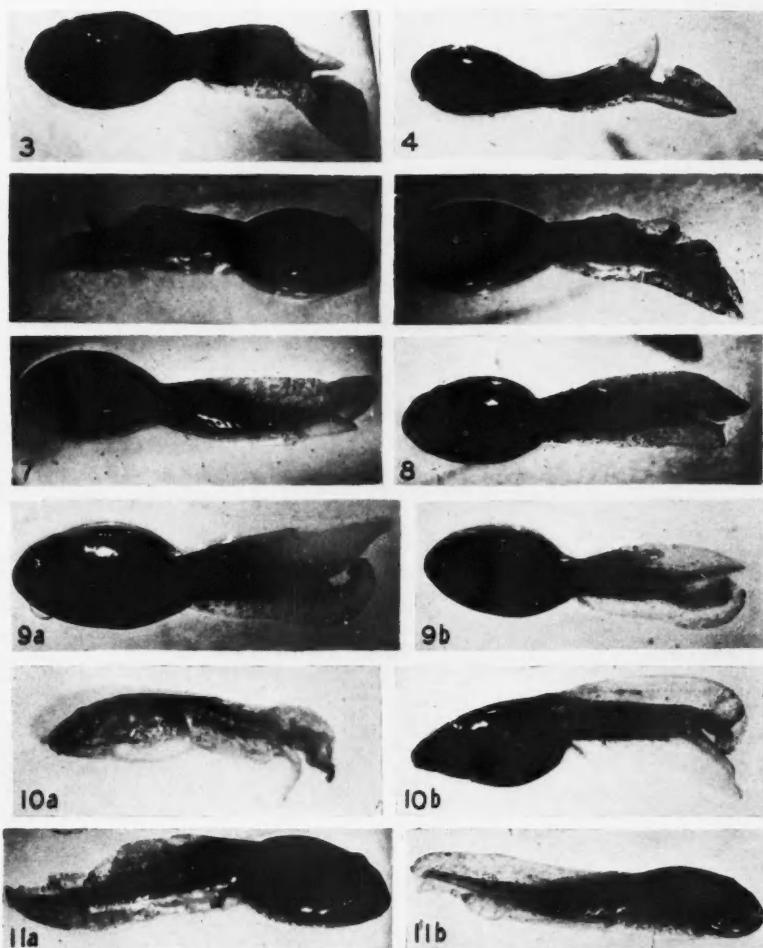
Similar injuries to the ventral edge of the tail gave substantially the same results. There was regeneration from both surfaces of the wound when the notochord was severed. When the notochord was not injured a nearly normal tail resulted.

In these cases, however, the nature of the accessory tail (Figs. 7, 8) depended upon the extent of the injury. If the cut was sufficiently deep to injure the nerve cord, both nerve cord and notochord appeared in the regenerate. If the nerve cord was not injured it was not observed in the accessory tail. Muscle fibers were always present, but less than the normal amount. The regenerating caudal vessels produced many small branches and were, therefore, small and irregular in the regenerate.

METHOD II

Thirty cases were studied in the following manner. In half the cases the dorsal half of the distal one-third of the tail was cut out in such a way as to include approximately half of the notochord (Fig. 2e). In the other half of the cases similar amounts of tissue were removed from the ventral side of the tail (Fig. 2f). Subsequent regeneration was dependent upon how the cuts removing the tissue were made.

If the transverse cut was made nearly perpendicular to the notochord, or at an obtuse angle with it, an accessory tail regenerated from that surface of the wound (Figs. 9a, 9b; 10a, 10b). If, however, this cut was made so that the exposed surface made an acute angle with the long surface of the injury,



FIGS. 3, 4, AND 5. Photographs (about $1.0\times$) to show the dorsal accessory tails produced following the injuries shown in Figs. 2a and 2b. Note the slight regeneration from the posterior surface of the wound in Figs. 3 and 4.

FIG. 6. Photograph (about $1.0\times$) to show the overlapping regenerates when the injury was nearly in the middle regions of the tail.

FIGS. 7 AND 8. Photographs (about $1.0\times$) showing the ventral accessory tails regenerated from the ventral injuries shown in Figs. 2c and d.

FIG. 9. Photographs (about $1.0\times$) to show the dorsal accessory tails following the removal of tissue as shown in Fig. 2e.

FIG. 10. Same to show ventral accessory tails. Fig. 10a is a poor photograph but is used here to show a distinct but peculiar accessory tail.

FIG. 11. Photographs (about $1.0\times$) showing the nearly normal tails resulting when the notochord is not injured by the operation. Note over-regeneration of the ventral fin in b. In a the notochord had been injured slightly and had regenerated dorsally. The notochord is the dark line in the dorsal fin near the tip of the tail.

NOTE: In the photographs the regenerates can be easily distinguished by the absence of pigmentation in the new tissues.

PLATE II

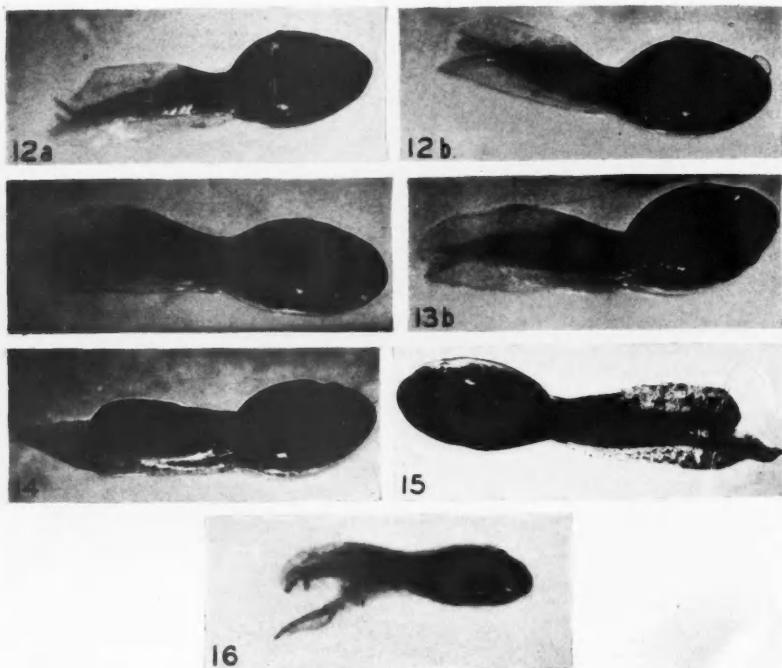


FIG. 12. Photographs (about $1.0\times$) to show the bifurcated tails following the operation shown in Fig. 18a. The ventral branch of the tail was the first regenerates.

FIG. 13. Same showing the nature of regeneration following the operation seen in Fig. 18b. The dorsal branch was the first regenerates.

FIG. 14. Photograph (about $1.0\times$) to show that the upper branch of the split tail degenerated when deprived of notochord. Note that the lower branch is nearly complete.

FIG. 15. Same showing partial degeneration of the upper part, and regeneration of the lower part of the split tail.

FIG. 16. Same showing that both branches persist and regenerate when each contains a part of the notochord.

the part removed was replaced by regeneration and a nearly normal tail resulted. Similarly, nearly normal tails were obtained if the notochord was uninjured (Figs. 11a, 11b).

In those cases that produced accessory tails from the transverse surface of the wound the old tail end was completed by regeneration from the long surface.

When the injury was made dorsally the nerve cord was injured in every case but the caudal vessels were not. The resultant accessory tails possessed a nerve cord, a notochord, and some muscle, but no definite caudal vessels. The ventral fin was usually lacking. The old tail end contained a notochord completed by regeneration and the original caudal vessels. In some cases fragments of nerve cord were accidentally left behind; these regenerated to produce a more or less complete nerve cord.

In one case the notochord was not injured but a regenerating tube of skin that had become infolded in some way served as a supporting axis for the accessory tail (Fig. 17). Outwardly, this regenerate did not appear different from the others.

When the ventral part of the tail was removed the transverse surface of the injury again produced an accessory tail and the old tail end was repaired by regeneration from the long surface. In most cases the nerve cord was not injured, but in a few cases the accessory tail contained a nerve cord when that structure had been accidentally severed. Otherwise, only the notochord was present. In every case definite but irregular caudal vessels appeared in the regenerate. Usually the dorsal fin was lacking. The old tail end contained the nerve cord and a notochord completed by regeneration. Definite caudal vessels were absent. As before, some muscle fibers were present in both the accessory tail and the old tail end.

METHOD III

Efforts to obtain accessory tails by a double amputation of the tail were made on 60 tadpoles. This method was a modification of that used by Dawson (3) to obtain a ventral accessory tail in *Triturus viridescens*.

In half of these cases the tip of the tail was amputated obliquely (Fig. 18a) so that the injured surface was directed ventrad. Resulting terminal regeneration produced a ventrally directed tail tip. When the regenerate was well established but before it had become regulated to its normal axis, a portion of the dorsal edge of the tail was removed at the point of deflection of the new tail tip (Fig. 18a). The ventrally directed regenerate continued its growth and a dorsal accessory tail was produced from the site of the second injury (Figs. 12a, 12b). This method was successful in relatively few cases because of the difficulty of making the second injury at just the right time and location. To ensure success the first regenerate had to be considerably deflected and the second injury made at just the angle of deflection and deep enough to injure the notochord. In most cases failure to obtain accessory tails was caused by the rapid regulation of the first regenerate to its normal axis.

In all cases in which accessory tails were obtained the ventral branch was complete since it was a normal terminal regenerate. The dorsal branch of the tail contained a nerve cord and a notochord accompanied by muscle fibers. Blood vessels were present but very irregular. Both branches of the tail were usually contained within a common fin fold.

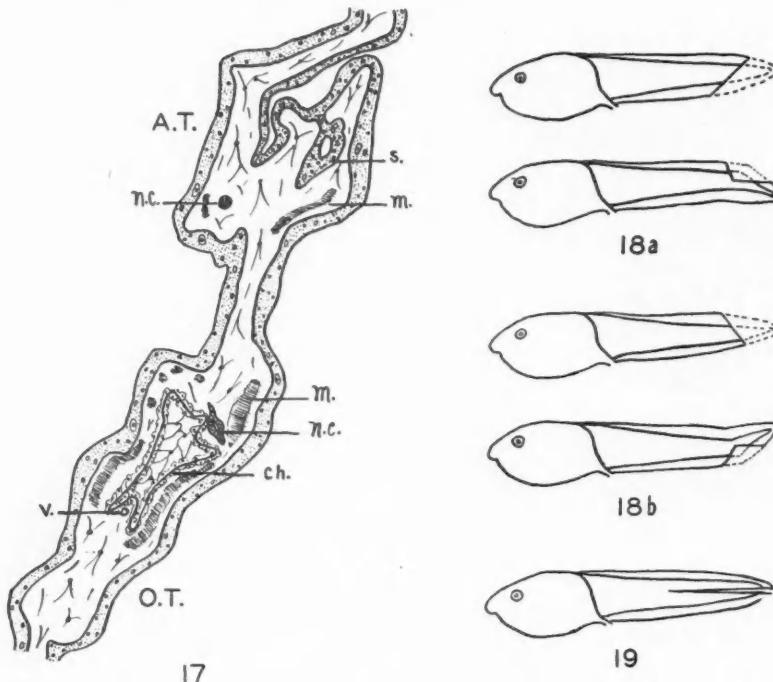


FIG. 17. Camera lucida drawing ($ca. 15\times$) of a transverse section of the tail of a tadpole such as that shown in Fig. 9a, b showing that the accessory tail in one case was supported by a fold of skin.

A.T. = accessory tail; O.T. = old tail; m. = muscle; s. = infolded tube of skin; n.c. = nerve cord; ch. = notochord; v. = caudal vessel.

FIG. 18. Line drawings to show the two successive operations described in Method III. Dotted lines indicate amount of tissue removed.

FIG. 19. Line drawing to show how the tail was split longitudinally in Method IV.

Similar results were obtained and the same difficulties encountered if the tip of the tail was amputated so that the amputation surface was directed dorsad (Fig. 18b) and a portion of the ventral edge of the tail was cut out at the angle of deflection (Fig. 18b).

When bifid tails were obtained in these cases (Figs. 13a, 13b) the upper branch was the first regenerate and therefore complete. The lower branch regenerated from the site of the second injury and its nature depended upon the extent of that injury. If the second cut was sufficiently deep to injure

the nerve cord, it regenerated and appeared in the lower branch. Otherwise, the nerve cord could not regenerate and was, therefore, absent from the lower branch. In all cases the ventral branch of the tail contained a notochord, muscle, and irregular vessels. Both branches of these tails were also contained within a common fin fold.

METHOD IV

One of Barfurth's (2) experiments was repeated on 15 tadpoles with a small measure of success. The tail was split longitudinally, parallel to the lateral line (Fig. 19). An attempt was made to split the notochord in half, whereas Barfurth attempted to separate the nerve cord from the notochord. Such a condition is extremely difficult if not impossible to obtain because of the close relationship between these structures and the opacity of the muscle mass.

A variety of results were obtained from this experiment. In many cases the halves of the tail healed together and the results were unsatisfactory. In two cases the dorsal portion of the split tail was deprived of notochord by the operation. In both cases, the upper part shrivelled and degenerated (Fig. 14), even though some nerve cord was present. The ventral portion regenerated a nearly normal tail including a dorsal fin.

In some instances the notochord was successfully split nearly in half. Under these conditions both halves of the tail not only persisted but regenerated (Figs. 15, 16). The upper portion contained a nerve cord, and a notochord completed by regeneration, and muscle fibers. The lower half contained a completed notochord, muscle, and caudal vessels. When the cut was irregular and fragments of nerve cord were left behind in the lower portion of the tail, a new nerve cord regenerated from the fragments.

In at least one case the notochord was isolated from the upper portion of the tail but a scar of skin tissue formed a sufficient support to maintain that part.

SURVEY OF RESULTS

Accessory tails or bifid tails are relatively easily produced in *Rana clamitans* tadpoles, and possibly in those of other species. It is interesting to note the great capacity for regeneration in this structure, particularly in view of the absence of regenerative capacity in the adult. It was frequently observed in these experiments that a great deal more tissue was produced by regeneration than was lost by injury, although this is not usually true in cases of normal terminal regeneration. The notochord is particularly capable of over-regeneration. This phenomenon probably accounts for the production of accessory tails. These observations support the opinion held by Barfurth that an accessory tail is an independent product of regeneration and not an incomplete reduplication of the tail.

Accessory tails produced by experimental methods were never histologically perfect and not always complete. The caudal vessels were always abnormal and atypically branched. This condition has also been reported by Fukai (5)

for other species of frog and toad tadpoles. The notochord was rarely cylindrical but showed irregular contours even when great care was taken with the preparation of the tails for study. Muscle was never as abundant in the accessory tail as it was in the old tail. The nerve cord frequently showed several branches, particularly when it was derived from fragments.

However, accessory tails always contained a notochord and muscle fibers, were nourished and innervated in some way, and were, therefore, functionally adapted. As such they are true tails, independent products of regeneration, and not simply reduplications of the tail.

Accessory tails arise only when the notochord has been previously injured so that it can regenerate in two directions or in two places simultaneously, except in those cases in which the old tail end was incompletely severed. In a very small number of cases a fold of skin had served as a supporting axis for an accessory tail in the absence of the notochord. Accessory tails can be produced in the absence of injury to the nerve cord, that is, in the absence of a regenerating nerve cord.

Discussion

In most groups of animals in which experiments have been carried out it has been acceptably demonstrated that regeneration of a part is dependent upon the presence of at least some nerve fibers at the cut surface. In the work cited in the Introduction none of the authors have obtained a completely nerveless tail stump. There is no direct evidence that regeneration of the tail of the frog tadpole is independent of the nervous system. Repetitions or modifications of the same experiments have been equally unfruitful. The writer's experiments show that under certain conditions of injury accessory tails arise when the nerve cord itself has not been injured. Such accessory formations, in most cases, resembled a normal tail end but were lacking a central nerve cord. It has already been stated that the distal half of the tail is innervated from ganglia situated in the proximal half. It is obvious, then, that there were always nerve fibers present at the cut surface even though the nerve cord had not been injured at that region. It may be justly inferred from this evidence that regeneration of the distal portion of the tail of the frog tadpole is independent of the presence of a cut central nerve cord at the amputation surface; that this structure neither initiates the regenerative process nor induces the formation of a tail. However, there is no evidence to suggest that this phenomenon is entirely independent of peripheral nerves. There is also the possibility that some influence is diffused from the intact nerve cord that becomes less active with distance from it.

It has been more clearly demonstrated that notochordal tissue induces tail formation in embryos of urodeles and anurans. Experiments on older anuran larvae seem to indicate that the presence of the notochord at the cut surface is essential to direct regeneration of the tail. The work of Wintrebert is probably the most significant. The results of his experiments seem to indicate that it is not merely the presence of the notochord but its function

as a supporting axis that is involved in regulating tail regeneration. Accessory tails arise only when the notochord has been severed or partially severed, with the possible exception of one or two cases (Fig. 17) in which a fold or tube of skin functioned in lieu of the notochord. When the notochord was not injured a nearly normal tail was regenerated. This fact supports Wintrebert's point of view that the notochord is essential to tail regeneration in frog larvae as a supporting axis around which new tissues are produced to form a tail.

Conclusions

It is generally accepted that the tissues of the tadpole tail in regeneration are derived from previously existing tissues by a process of dedifferentiation, properly called modulation. That is, new muscle is derived from preexisting muscle, nerve cord from nerve cord, and notochord from notochord, and not from an indifferent blastema. Studies of accessory tail formation further support this point of view.

Any structure that is isolated from a part of the tail by mutilation does not appear in the regenerate. Accessory tails can be produced that lack a central nerve cord, notochord, or caudal vessels. This is taken to mean that, if any of these structures are isolated from the injured region, the regeneration blastema formed at the injured surface does not contain elements for their formation. In other words, the blastema is not composed of indifferent elements. For this reason, injury that includes only muscle and connective tissue, with some nerves and small blood vessels, does not produce an accessory tail, since there is no source of a supporting notochord.

Since there is some regeneration of tail tissues in the absence of injury to the notochord, it is obvious that regeneration is not dependent upon the presence of the notochord at the cut surface. The notochord does not initiate the regenerative process but its function as a supporting axis secondarily directs the formation of a tail and therefore is essential to the regeneration of a tail. From the evidence available it may be inferred that regeneration in the distal part of the tail is independent of the central nerve cord. There is no evidence to suggest that the peripheral nervous system as represented by nerve fibers at the cut surface has no influence on the process of regeneration, although it has been assumed by some that the influence of the nervous system is probably negligible. However, in view of the evidence obtained in studies of regeneration by many careful and methodical workers, in both invertebrates and vertebrates it cannot be said with certainty that regeneration of the tail of the frog tadpole is entirely free of some influence of the nervous system. Further experimentation is necessary to determine the extent of nervous influence and to explore the possibility of a histochemical influence (perhaps active through nerve fibers) on tail regeneration in frog tadpoles.

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**A COMPARATIVE STUDY OF THE PROVENTRICULUS OF
ORTHOPTEROID INSECTS WITH REFERENCE TO
ITS USE IN TAXONOMY¹**

BY W. W. JUDD²

Abstract

The structure of the proventriculus in 115 species of orthopteroid insects (eight orders) is investigated.

The Blattodea, Mantodea, and Isoptera have a conical proventriculus, with 6 or 12 longitudinal teeth. There are eight tubular gastric caeca. The Ensifera (Gryloidea and Tettigonoidea) have a globular proventriculus with a tubular neck. In the globular part are six longitudinal folds each bearing a series of appendages and separated from one another by partitions. There are two bulbous gastric caeca. The four families of the Caelifera have a tubular proventriculus. The Acrididae have six longitudinal plates in the proventriculus and six gastric caeca with anterior and posterior projections. The other three families have no plates in the proventriculus. The Tridactylidae have two gastric caeca, the Tetrigidae have six short, conical caeca, and the Cylindra-chaetidae have six long, tubular caeca.

The Phasmida have a tubular proventriculus with longitudinal, spine-bearing folds and a long flaplike oesophageal valve. In the Grylloblattaria the organ is globular with 12 longitudinal folds in the intima, and two ranks of 12 pyramidal teeth at its posterior end. The Dermaptera have a tubular proventriculus, flared slightly where it joins the crop. Internally there are six longitudinal folds bearing small scalelike projections, and a cushion of bristles at the anterior end of each fold. In the Plecoptera the proventriculus is tubular, with 14 longitudinal, spine-bearing plates on its inner surface. There are seven tubular gastric caeca.

A 'phylogenetic tree' demonstrates the relationships of the groups studied, and a systematic key is prepared.

Introduction

The proventriculus, as the term implies, is the region of the fore-gut that lies immediately in front of the ventriculus or mid-gut of insects. In common with the rest of the fore-gut or stomodaeum it is ectodermal in origin, being lined with a sclerotized intima, in contrast to the mid-gut, which is endodermal in origin and which has no sclerotized intima. As will be shown in subsequent descriptions, the proventriculus displays all degrees of development from a simple valve lined with soft cuticle to a powerful muscular organ armed with spines and teeth.

While the term proventriculus is properly applied only to the posterior region of the fore-gut, some authors use it with reference to a swollen region of the mid-gut of Diptera. Snodgrass (105) shows that this is not truly a proventriculus since it is not ectodermal in origin and since the oesophageal valve projects into its anterior end, instead of projecting from its posterior end into the mid-gut. The work of several authors on Diptera confirms this

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view (8, 38, 59, 60, 65, 72, 120). In some Diptera, notably in *Drosophila melanogaster*, the 'proventriculus' is composed of both ectodermal and endodermal tissues (96, 118). Among the Homoptera (Coccidae (74), Cicadidae (62, 63)) the region described as proventriculus is also of endodermal origin. In the Heteroptera the whole fore-gut is reduced in size (20, 58) although the oesophageal valve is well defined in some cases. It is thus to be seen that a specialized proventriculus in the fore-gut of sucking insects is rare. The most important exception to this generalization is in the Siphonaptera of which several species have a globular proventriculus lined with spines (19, 48, 86, 118).

It is in mandibulate insects that the proventriculus shows the widest diversity in structure. This wide diversity has led to investigations along three main avenues:

1. Correlation of the structure of the proventriculus with the feeding habits of insects.
2. Function of the proventriculus.
3. Study of the proventriculus as a structure to be used in classification of insects and in the investigation of phylogenetic relationships.

It is the purpose of the present writer to compare the structure of the proventriculus in various groups of orthopteroid insects with a view to determining what light this study may throw upon the phylogenetic relationships existing among these groups, and to investigate what use it may be in taxonomy. Conclusions concerning the phylogeny of insects have been based mainly upon consideration of the external anatomy, but, in the words of Walker (112), "in any attempt to unravel the relationships of a group of organisms it is obvious that the entire structure of the body should be taken into account".

System of Classification

In the 10th edition of his *Systema Naturae* Linnaeus (80) erected, in the order Insecta Coleoptera, three genera: *Forficula*, *Blatta*, and *Gryllus*, which correspond to the Dermaptera of DeGeer (39) and the Orthoptera of Olivier (85). To the first two of these he assigned a number of species and the last he divided into six subgenera: *Mantis*, *Acrida*, *Bulla*, *Acheta*, *Tettigonia*, and *Locusta*. Fabricius (49) adopted the generic names *Forficula* and *Blatta* and used the name *Gryllus* to designate Linnaeus' *Gryllus Locusta*, and the other five of the subgenera of Linnaeus' *Gryllus* he used as genera, changing the names of three of them: *Mantis*, *Truxalis* (*Acrida* L.), *Acrydium* (*Bulla* L.), *Acheta*, *Locusta* (*Tettigonia* L.). Stoll (106) adopted a classification similar to that of Linnaeus but divided the genus *Mantis* into two, *Mantis* and *Phasma*.

Leach (79) restricted the use of the name Dermaptera to the order of earwigs (*Forficula*) and included the cockroaches in the order Dictyoptera, the mantids in the order Mantida, and the walking-sticks in the order Phasmida. He assigned the crickets to a family of Achetidae, the long-horned

grasshoppers to a family Gryllidae, and the locusts to a family Locustidae. Burmeister (23) adopted a similar classification and used the following terms: Blattina (cockroaches), Mantodea (mantids), Phasmodea (walking-sticks), Gryllodea (crickets), Locustina (long-horned grasshoppers), Acridiodea (locusts). Karsch (77) adopted a classification similar to that of Burmeister but used the terms Phasgonuridea and Acridodea in place of Burmeister's Locustina and Acridiodea. Handlirsch (55, 56) in his exhaustive study of fossil insects established two superorders: Orthopteroidea and Blattaformia. The former comprised the orders Orthoptera (suborders Locustoidea and Acri-
dioidea), Phasmoidea, and Dermaptera and the latter the orders Mantoidea, Blattoidea, and Isoptera.

The inclusion of the Phasmoidea and Dermaptera with the Orthoptera in a superorder Orthopteroidea implies a close relationship among these three groups. That this relationship exists is disputed by some authors, and in this treatment the superordinal terms will not be used. The names of the orders adopted are then: Blattodea, Mantodea, Isoptera, Phasmida, Orthoptera (Saltatoria), Grylloblattaria, Dermaptera, and Plecoptera.

Ander's classification of the Saltatoria (1), based upon his phylogenetic studies has been adopted, and Roberts' (95) classification of the Acrididae based upon his study of phallic structures has been adopted.

The classification, to subfamily, of the forms investigated in this study is then as follows:

Order Blattodea

Family Blattidae

- Subfamily Pseudomopinae
- " Blattinae
- " Panchlorinae
- " Blaberinae
- " Panesthinae

Order Mantodea

Family Mantidae

- Subfamily Mantinae
- " Liturgousinae
- " Oligonicinae
- " Photininae

Order Isoptera

Family Termitidae

- Subfamily Calotermitinae

Order Phasmida

Family Phasmidae

- Subfamily Bacunculinae
- " Phibalosominae
- " Anisomorphinae

Order Orthoptera (Saltatoria)

Suborder Ensifera

Superfamily Grylloidea

Family Gryllotalpidae

" Gryllidae

Subfamily Oecanthinae

" Trigonidiinae

" Nemobiinae

" Gryllinae

" Myrmecophilinae

" Mogoplistinae

" Eneopterinae

Superfamily Tettigonioidea

Family Tettigoniidae

Subfamily Phasgonurinae

" Phaneropterinae

" Copiphorinae

" Conocephalinae

" Decticinae

Family Stenopelmatidae

Subfamily Stenopelmatinae

" Henicinae

Family Rhaphidophoridae

" Prophalangopsidae

Suborder Caelifera

Superfamily Tridactyloidea

Family Tridactylidae

" Cylindrachaetidae

Superfamily Acridoidea

Family Acrididae

Subfamily Acridinae

" Oedipodinae

" Romaleinae

" Cyrtacanthacrinae

Family Tetrigidae (Acrydiidae)

Subfamily Tetriginae

" Batrachidinae

Order Grylloblattaria

Family Grylloblattidae

Order Plecoptera

Family Perlidae

Order Dermaptera

Family Labiduridae

Historical Review

Since Linnaeus (80) based his classification of insects upon the structure of the wings, and Fabricius (49) based his upon the structure of the mouth parts, the search for an adequate basis of classification has continued. This has led to extensive comparative studies of the various organ systems of insects. Many authors have made such studies in the Orthoptera and have derived therefrom schemes to show the phylogenetic relationships existing among the various groups.

Bordas (14, 16) studied the structure of the alimentary canal of orthopteroid insects and divided them into two groups, the Acolotasia, with no diverticula or appendages at the mid-gut, and the Colotasia with one or more diverticula at the anterior end of the mid-gut. Later (18) he published an account of a comparative study of the nervous system of representatives of the families of the Orthoptera. He found that in the Blattidae and Mantidae there were unpaired abdominal ganglia and that in the Gryllidae, Tettigoniidae, and Acrididae there were paired abdominal ganglia.

Jensen (73) studied the spermatophores of the Gryllidae and concluded that they are of value in distinguishing the species of *Gryllus* from one another.

The chromosomes of the Tetrigidae and the Acrididae were studied by Robertson (97). He found that these two families had chromosomes of characteristic number, and that the genera of the Tetrigidae could be divided into two groups on the basis of the size of the chromosomes.

Walker (111, 112) investigated the terminal abdominal structures of male and female orthopteroid insects. His conclusions were expressed in a 'phylogenetic tree' in which the blattids, mantids, and termites were closely associated, and the 'Orthoptera' consisted of the long-horned grasshoppers, crickets, sand crickets, and locusts. The Grylloblattoidea and Phasmoidea were shown to be more closely related to the blattoid insects than to the Orthoptera.

Crampton (29, 31, 35) used several external characters in his comparative studies of the Orthoptera. His conclusions were somewhat similar to those of Walker but he considers that the Phasmids and Dermaptera are more closely related to the Orthoptera than to the blattoid insects.

Ford (53) studied the abdominal musculature of the orthopteroid insects. She concluded that "the dispositions of the muscles confirm the relationship of the Blattaria with the Mantaria, Phasmaria and Grylloblattaria, although the latter order resembles considerably the Orthoptera".

Ohmachi (84) divided the Grylloidea into two groups, basing his conclusions upon a study of the chromosomes.

Handlirsch (56, 57) in his exhaustive study of the fossil record divided the orthopteroid insects into two superorders, Orthopteroidea and Blattaeformia, each of which included several orders.

Karny (75) studied the phylogeny of the Ensifera and concluded that the Acridoidea and Grylloidea were derived from ancestors similar to the genus *Gryllacris*.

The external characters of the digestive tracts of species of *Tridactylus*, *Cylindroryctes*, *Acrydium*, and *Gryllotalpa* were investigated by Carpentier (27). He concluded that *Tridactylus* was properly classified with *Cylindroryctes* and *Acrydium* rather than with *Gryllotalpa*.

In his *Anatomie and Phylogenie of the Ensifera*, Ander (1) studied the internal and external anatomy of these insects. His results show that the Ensifera and Caelifera form two distinct groups although they are commonly associated in the order Saltatoria. Zeuner (122) also investigated the Ensifera basing his study upon the fossil record. His conclusions concerning the relationship of the Ensifera to the Acridoidea are similar to those of Ander.

Slifer (102, 103) studied the internal genitalia of female Acrididae and classified the Acrididae on the basis of the structure of the diverticula of the spermathecae and the glandular pouches of the genitalia.

The nervous system of orthopteroid insects was the subject of a comparative study by Nesbitt (83). He divided them into two groups on the basis of the number of posterior recurrent nerves: (i) with one recurrent nerve: Mantidae, Blattidae, Phasmatidae, Grylloblattidae, Isoptera, Dermaptera; (ii) with two recurrent nerves: Tettigoniidae, Rhaphidophoridae, Gryllidae, Acrididae.

Rau (93) discussed the derivation of termites from cockroaches as revealed by study of their method of oviposition and habits.

Roberts (95) drew up a scheme, based primarily upon a study of the phallic structures, to show the relationship of the subfamilies of the Acrididae to one another, and Isely (71) made a comparative study of the mandibles in the same family.

Walker (113, 114, 116, 117) studied the structure of several systems of *Grylloblatta campodeiformis* Walker and emphasized the relationship of the Grylloblattaria with the Saltatoria, especially the Ensifera, rather than with the Blattodea, Mantodea, and Isoptera, the view which he previously expressed (111, 112).

Material and Technical Methods

MATERIAL

The proventriculus in 115 species of insects is studied: Blattodea—12; Mantodea—6; Phasmida—4; Orthoptera (Grylloidea—18; Tettigonioidea—34; Caelifera—37); Grylloblattaria—1; Isoptera—1; Plecoptera—1; Dermaptera—1. The description of the intima of the proventriculus of each species is, in most cases, based upon the study of a single whole mount.

MEASUREMENTS

Measurements of structures were made with the aid of an ocular micrometer in the ocular of a compound microscope. The dimensions of structures in the intact digestive tract and in whole mounts are approximate and are given in centimeters and millimeters. The dimensions of structures in stained microscopic sections are given in millimeters or microns (μ).

WHOLE MOUNTS

Whole mounts were prepared to show the sclerotized lining of the proventriculus flattened out and divested of connective tissue and muscles. They were prepared from pinned specimens and specimens preserved in alcohol.

The alimentary canal of a preserved specimen was removed from the body and pinned down, by means of pins through the crop and mid-gut, to a layer of wax in a Syracuse watch glass. The alimentary canal was then covered with water, and was slit longitudinally with a pair of fine eye scissors, this operation being accomplished with the aid of a binocular microscope. The proventriculus was then cut from the alimentary canal, and its muscular coat was removed by careful manipulation with fine needles. In some cases the muscle could not be removed by this method, so the proventriculus was placed for about 12 hr. in a strong solution of potassium hydroxide, which dissolved the muscles.

Pinned specimens were placed in a solution of potassium hydroxide for about 12 hr. The pin was then carefully withdrawn and the dorsal body wall of the insect was cut longitudinally with eye scissors. The sclerotized lining of the proventriculus was removed from the body cavity and was slit longitudinally. Any soft tissues remaining attached were removed with fine needles or by placing the proventriculus in potassium hydroxide for a few hours.

The sclerotized lining of the proventriculus, divested of muscles and other soft tissues, was washed with water to remove the potassium hydroxide. It was then placed in several changes of alcohol of increasing concentrations to remove water, and finally in absolute alcohol. The absolute alcohol was washed out with xylol, and the sclerotized lining was mounted on a slide in Canada balsam or clarite.

LONGITUDINAL SECTIONS AND TRANSVERSE SECTIONS

The alimentary canals of large newly-killed specimens were removed under water, with the aid of a binocular microscope and were immediately placed in Bouin's fixative. Small, soft insects were carefully opened along the mid-dorsal line and placed in the fixative. The specimens were left in the fixative for from six hours in the case of the smallest insects to 20 hr. in the case of the largest insects. They were then cleared of fixative by repeated changes of 70% alcohol and were stored in 70% alcohol. After being embedded in wax and sectioned at 10μ with a rotary microtome, the tissues were stained with Haidenhain's haematoxylin and counterstained with eosin. By this process nuclei were stained blue, muscles and connective tissue were stained red, while exocuticle remained yellow or brown.

Descriptions of Types

BLATTODEA

BLATTIDAE

Historical Note

Authors who first studied the function of the digestive tract of insects worked on large insects of common occurrence such as the cockroaches. Of these, *Blatta (Periplaneta) orientalis* Linnaeus has received a great deal of attention and consequently the structure of its digestive tract has been thoroughly investigated by several authors: Basch (5), Miall and Denny (81), Visart (110), Bordas (13, 16), Petrunkevitsch (88), Ramme (92), and Eidmann (45).

Cuénnot (36) studied the physiology of orthopteroid insects and illustrated his work with a longitudinal section of the digestive tract of *Ectobia perspicillaris* Herbst. (*E. livida* Fabricius). A short description of the proventriculus of *Blattella germanica* Linnaeus was given by Ross (98).

In his comparative study of the digestive tracts of Orthoptera, Bordas (10, 13, 16) investigated a number of species of cockroaches. He described briefly the structure of the proventriculi and arranged the species in four groups in accordance with the complexity of structure of the proventriculus.

Original Descriptions

*Pseudomopinae**Parcoblatta pennsylvanica* DeGeer

The proventriculus (Fig. 1-P) is conical in shape with the crop (C) leading into the broad end of the cone and the apex of the cone leading into the mid-gut (MG) the anterior end of which bears eight tubular gastric caeca (GC). The proventriculus is 1.5 cm. long. In the anterior region of the proventriculus there are six sclerotized teeth (Fig. 13—CT) projecting into the lumen. Each tooth is flattened laterally. Midway along its length it bears a sharp spine (S), which projects posteriorly. Behind this spine the tooth broadens out slightly and bears much smaller closely-set spines (Ss) projecting posteriorly. Between each pair of teeth there are seven parallel folds projecting slightly into the lumen and bearing fine hairs. The middle, primary fold (PF) is the longest of the seven and extends posteriorly well beyond the posterior limit of the teeth. At either side of the primary fold there are three secondary folds (SF) that are shorter and narrower than the primary folds. Behind each tooth there is a pair of cushions bearing closely-set hairs and projecting into the lumen. The anterior cushion (AC) is 0.3 mm. long and its width is slightly less than its length. The posterior cushion (PC) is 0.2 mm. wide at its anterior end and tapers gradually to join the oesophageal valve (Oes. V.).

Longitudinal section and transverse section (Figs. 14, 15).—The inner layer of the proventriculus is a sclerotized intima (I). On the teeth (CT) it is most heavily developed, particularly in the spine (S) of the tooth where it is 20 μ

in thickness. On the anterior cushions (AC) it is thin (3 to 4 μ) and bears closely-set hairs (H). Beneath the intima is a layer of epithelial cells (EP). Throughout the length of the proventriculus this layer is 15 to 30 μ thick and is continuous with the epithelial layer of the oesophageal valve (Oes. V.). Next to the epithelial layer is the longitudinal muscle (LM). In the anterior region of the proventriculus it is two or three fibers in thickness, while in the teeth it is six to eight fibers in thickness. Some of these fibers extend obliquely as retractor muscles (RM) and are connected with the epithelium below the intima of the teeth. Outside the longitudinal muscle is a layer of circular muscle (CM). This is most strongly developed in the region of the teeth, being six to eight fibers in thickness, and less well developed in the posterior region of the proventriculus, being two to three fibers in thickness.

Blattella germanica Linnaeus

Aglaopteryx gemma Hebard

Ischnoptera deropeltiformis Brunner

Supella supellectilium Serville

Cariblatta lutea lutea Saussure and Zehnter

The proventriculus in these species is similar to that of *Parcoblatta pennsylvanica* except in size. In *B. germanica* it is 0.5 mm. long; in *A. gemma*, 0.4 mm. long; in *I. deropeltiformis*, 0.9 mm. long; in *C. l. lutea*, 0.4 mm. long; and in *S. supellectilium*, 0.6 mm. long.

Blattinae

Periplaneta americana Linnaeus

The proventriculus is conical and 3.5 mm. long. The anterior half is occupied by six heavily sclerotized teeth (Fig. 18, CT), which are 1.5 mm. long and project into the lumen of the proventriculus. The base of each tooth is roughly rectangular and 0.5 mm. wide. The teeth are of such a shape that when the proventriculus is intact they fit snugly together at their tips, leaving six channels between the bases. Two of these teeth, 1 and 5, are mirror images of one another with a strong projection midway along their length. Two other teeth, 2 and 4, are mirror images of one another and are grooved laterally. Tooth 3 has a flat surface toward the lumen of the proventriculus and has a groove at the tip on each side. In the intact proventriculus it opposes Tooth 6, which has a curved spine at its anterior end and a small groove at each side midway along its length. Between each pair of teeth there are three parallel folds projecting slightly into the lumen, and bearing fine hairs. The middle or primary fold (PF) is 1.5 mm. long and the secondary folds (SF) are slightly shorter. Following each tooth there is a pair of cushions bearing close-set hairs. The anterior cushion (AC) is 0.5 mm. long and square at its base. The posterior cushion (PC) is 0.5 mm. broad anteriorly and 1 mm. long and tapers gradually to a point where it reaches the oesophageal valve (Oes. V.). Between the anterior ends of each adjacent pair of posterior cushions there is a small secondary cushion bearing hairs (SC).

Eurycotis floridana Walker

In this species the proventriculus is similar in all respects to that of *Periplaneta americana* except that it is slightly larger, being 4 mm. long.

Blatta orientalis Linnaeus

In this species the proventriculus is similar in all respects to that of *Periplaneta americana* except that it is considerably smaller, being 2 mm. long.

*Panchlorinae**Pycnoscelus surinamensis* Linnaeus

The proventriculus is conical and 1 mm. long. In the anterior end there are six small teeth (Fig. 16—CT). They are about 100μ long and slightly less in width. At its base and toward its posterior end each tooth bears small spines, and projecting into the lumen of the proventriculus there is a large spine (S). Each tooth is situated on the anterior end of an ovoid patch (OP) bearing closely-set bristles. This patch is 0.5 mm. long and tapers posteriorly to a point. Between each pair of these patches there is a single primary fold (PF) similar in shape to the ovoid patches, but shorter. Following each of the ovoid patches, there is a cushion (C) 0.05 mm. in width and extending to the oesophageal valve (Oes. V.).

*Blaberinae**Blaberus atropos* Stoll

The proventriculus is conical and 3 mm. long. In the anterior end are six teeth (Fig. 17—CT). The base of each tooth is roughly square and 0.2 mm. long. The tooth projects posteriorly in a broad spine and bears a few irregularly placed smaller spines. Beneath the spine the posterior surface of the tooth is concave. Each tooth is situated on a square patch covered with fine bristles (P). Between the patches there are six primary folds (PF) 1 mm. long and covered with fine bristles. Behind each patch are two cushions covered with bristles. The anterior cushion (AC) is 1 mm. long and 0.5 mm. wide. The posterior cushion (PC) is 1.5 mm. long and 0.5 mm. wide and tapers slightly toward the oesophageal valve (Oes. V.).

*Panesthinae**Cryptocercus punctulatus* Scudder

The proventriculus is conical and 2 mm. long. In the anterior end are six teeth (Fig. 19—CT) 0.5 mm. in length. The base of each tooth is rectangular and about 0.2 mm. wide. The heavily sclerotized portion of the tooth is a laterally flattened projection rising to a peak near the anterior end of the tooth. Between each pair of teeth there are seven folds, each equal in length to the teeth. The three primary folds (PF) are 0.1 mm. wide and the four secondary folds (SF) are 0.05 mm. wide. All seven are sclerotized and bear small overlapping spines. Behind each tooth there are two cushions. The anterior cushion (AC) projects into the lumen and bears two spines; the anterior spine (AS) is the larger and is surrounded by small spines at its base and over the surface of the cushion; the posterior spine (PS) is smaller

and is covered with smaller scalelike spines. The posterior cushion (PC) bears a spine similar to the posterior spine of the anterior cushion, and tapers gradually toward the posterior where it joins the oesophageal valve (Oes. V.).

M A N T O D E A

MANTIDAE

Historical Note

The structure of the proventriculus of the common mantid *Mantis religiosa* Linnaeus has been described by Visart (110), Bordas (16), and Ramme (92). Bordas also studied the digestive tract of several other species of Mantidae and described the proventriculus in *Tenodera australasiae* Leach, *Hierodula viridis* Forskal (*H. bioculata* Burmeister), *Stagmatoptera predatoria* Stoll, *S. annulata* Stoll, and *Eremiaphila denticollis* Lefebvre.

Original Descriptions

Mantinae

Mantis religiosa Linnaeus

In this species the proventriculus is conical and 2 mm. long (Fig. 2—P). Its broad end opens from the crop. Just posterior to its point of union with the mid-gut (MG) there are eight tubular gastric caeca (GC). On the inner surface anteriorly there are six areas of narrow longitudinal ridges (Fig. 20—AR). On each of these areas the ridges anastomose posteriorly toward a point midway in the length of the proventriculus where they end at a short cluster of hairs (CC). In transverse section (Fig. 22) the ridges are seen to be narrow and forked at their tips (FT) owing to the presence of grooves that run throughout the length of each ridge. Alternating with the areas of anastomosing ridges are six teeth (Fig. 20—CT) that run the length of the anterior half of the proventriculus. (Four of these are shown in the figure.) Directly behind each tooth there are two cushions. The anterior cushion (AC) is densely clothed with hairs and posteriorly may break up into three to five folds likewise clothed with hairs. The posterior cushion (PC) is elongated and clothed with hairs and extends posteriorly to the oesophageal valve (Oes. V.).

Transverse sections (through region of teeth—Fig. 21; through anterior cushions—Fig. 23; through anastomosing ridges—Fig. 22).—The innermost layer of the proventriculus is the intima (I), which is generally 20 μ thick, although slightly thicker over the teeth (CT), and appearing as forked projections (FT) in the anastomosing ridges. Over the anterior cushions the intima bears sharp hairs (CH). Beneath the intima is a single layer of epithelial cells (EP), 20 to 25 μ thick. Next to the epithelial layer is the longitudinal muscle (LM), which is several strands in thickness beneath the longitudinal teeth and in the anterior cushions. The outer layer of the proventriculus is circular muscle (CM), four to six fibers thick.

Stagmomantis carolina Johannsson

In this species the proventriculus is similar to that of *M. religiosa* but is larger, being 3 mm. long.

*Liturgousinae**Gonatista grisea* Fabricius

The proventriculus is similar to that of *M. religiosa* but is smaller, being 1.5 mm. long.

*Oligonicinae**Oligonicella scudderii* Saussure*Thesprotia graminis* Scudder

The proventriculus in these two species is similar to that of *M. religiosa* but is much smaller, being 1 mm. long.

*Photininae**Brunneria borealis* Scudder

The proventriculus is similar in size and structure to that of *M. religiosa*.

Terms Used by Authors in Describing the Proventriculus of Blattodea
and Mantodea

Sclerotized tooth:

- heavily chitinized tooth (Basch)
- anterior tooth (Bordas, Eidmann)
- chitinous tooth (Mantodea) (Bordas)
- tooth (Ross)

Anterior cushion:

- anterior cushion (Basch)
- posterior tooth (Bordas)
- first fold of posterior proventriculus (Eidmann)
- membranous cushion (Ross)

Posterior cushion:

- posterior cushion (Basch)
- muscular fold (Bordas)
- second fold of posterior proventriculus (Eidmann)
- band of muscle (Ross)

Primary fold:

- primary fold (Basch)
- flattened denticle (Bordas)
- principal fold (Eidmann)
- spatulate loop (Ross)

Secondary fold:

- secondary fold (Basch)
- flattened denticle (Bordas)
- smaller folds (Eidmann)

In Mantodea, anastomosing ridges (Bordas) are present in place of primary and secondary folds in Blattodea.

P H A S M I D A

PHASMIDAE

Historical Note

Bordas (12, 16) described briefly the structure of the crop and proventriculus of *Phibalosoma pythonius* Westwood, *Acanthoderus spinosus* Gray, and *Necroscia erectheus* Westwood. Of this part of the fore-gut he says "it can be homologized, from an anatomical point of view, with the gizzard of most Orthoptera".

Heymons (61) described the digestive tract of *Bacillus rossii* Fabricius and says that a "Kau—oder muskelmagen" is altogether absent.

deSinéty (40) described briefly the proventriculus of a species of Phasmidae and Cameron (24) described the proventriculus of *Bacillus rossii* Fabricius.

Original Descriptions

Bacunculinae

Diapheromera femorata Say

In this species the proventricular region is comparatively simple in structure (Fig. 3—P). It is cylindrical and continuous with the crop (C) and enters the mid-gut (MG) as a slender oesophageal valve (Fig. 25—Oes. V.). The inner surface of the crop and proventriculus is occupied by longitudinal folds (LF) 0.2 mm. in width. The surface of each fold is armed with small spines (Fig. 26—S) projecting into the lumen of the proventriculus. On each fold these spines are arranged in transverse rows with six in each row.

Longitudinal section (Fig. 24).—The inner layer of the proventriculus is the intima (I), which is composed of two layers. The innermost layer is 5 to 10 μ thick and bears the small spines. The second layer is 30 to 40 μ thick. Next to the intima is the epithelial layer (EP) of small irregular cells 25 to 50 μ thick. It extends throughout the crop, proventriculus, and oesophageal valve (Oes. V.) and is continuous with the much thicker (60 to 80 μ) epithelial layer of the mid-gut (MG). Outside the epithelial layer is a sparse layer of longitudinal muscle (LM) and outside this a layer of circular muscle (CM) three to five fibers thick. In some specimens the wall of the proventriculus shows a thick invagination (Inv.). Posterior to the proventriculus the oesophageal valve (Oes. V.) projects into the mid-gut as a long flap (FL).

Manomera tenuescens Scudder

The proventriculus in this species is similar to that of *D. femorata*.

Phibalosominae

Aplopus mayeri Caudell

The proventriculus is similar to that of *D. femorata*.

*Anisomorphinae**Anisomorpha buprestoides* Stoll

The gross structure of the proventriculus is the same as that of *D. femorata*. The surface of each longitudinal fold (Fig. 27—LF) bears rounded, irregularly-placed scales (S). Some of these are simple and others are larger and bear other smaller rounded scales.

Terms Used by Authors in Describing the Proventriculus of Phasmidae
Longitudinal folds:

- striated folds (Bordas)
- longitudinal folds (Bordas)

Small spines:

- small spines (deSinet)
- chitinous teeth (Bordas)

ORTHOPTERA

ENSIFERA

GRYLLOIDEA

Historical Note

The digestive tract of the European mole cricket, *Gryllotalpa vulgaris* Latreille, has been studied by several investigators and its proventriculus has been described by Wilde (119), Eberli (44), Cuénot (36), Bordas (16), and Ramme (92). The proventriculus of *Gryllotalpa australis* Erichson was described by Sayce (99), and Carpentier (27) noted the external features of the proventriculus of *Gryllotalpa gryllotalpa* Linnaeus.

The structure of the proventriculus of the field cricket, *Gryllus campestris* Linnaeus, was described by Graber (54) and by Berlese (6) who called it a "ventrilio". Graber also studied the organ in *Gryllus melas* and *Oecanthus pellucidus*. Wilde (119) described the proventriculus of the house-cricket, *Gryllulus domesticus* Linnaeus. Other members of the Gryllinae in which the proventriculus has been described are *Gryllulus pennsylvanicus* Burmeister (DuPorte (43)) and the Chinese cricket, *Gryllus mitratus* Burmeister (Hsu (69)), and in the Myrmecophilinae, a family of crickets inhabiting ant hills, the structure of the proventriculus of *Myrmecophila acervorum* Latreille has been investigated by Schimmer (100).

Bordas (11, 13, 18) described the proventriculus of several crickets and divided them into three groups on the basis of complexity of structure.

Original Descriptions

GRYLLOIDAE

*Oecanthinae**Oecanthus nigricornis* Walker

The proventriculus consists of a globular body (Fig. 4—P) joined to the crop (C) by a tubular neck. It lies between the two bulbous gastric caeca

(GC) of the mid-gut (MG). The lining of the proventriculus is organized into six longitudinal folds. In the neck each of these folds bears a series of lobes covered with hairs (Fig. 32—CL). In the globular part of the organ each fold bears a series of nine sclerotized appendages (CA). The anterior appendage in each series is 0.3 mm. wide and the size of the others decreases gradually toward the posterior appendage, which is 0.15 mm. wide. The central portion of each appendage is a median tooth (Fig. 40—MT), which projects into the lumen of the proventriculus and bears five or six pointed median denticles (MD). From the center of the base of the median tooth there is a pair of lateral teeth (LT) projecting posteriorly and bearing several short spines that project laterally. From the side of the median tooth and below the lateral tooth a lateral denticle (LD) extends outward and bears a few rounded lobes. Beneath these teeth and denticles there is a truncated lobe, the inner barbated lobe (IBL), which extends laterally. It is less heavily sclerotized than the other parts and bears fine bristles at its outer extremity. At each side of the appendage there is an outer barbated lobe. This has a roughly square base and tapers, toward the lumen of the proventriculus, to a blunt point (Fig. 32—OBL). Posterior to the last appendage in each longitudinal fold the oesophageal valve extends into the mid-gut and ends as a round flap (Oes. V.). Between adjacent longitudinal folds there is a partition (CP) coextensive with the series of appendages.

Transverse sections (through median tooth, Fig. 29; through median denticles, Fig. 30; through lateral teeth, Fig. 31).—The inner layer of the proventriculus is the intima (I). This is thickest where the teeth and denticles have lobes and spines as in the lateral teeth (LT) and lateral denticles (LD). Beneath the intima is the epithelial layer (EP) and beneath this the longitudinal muscle (LM), one to four fibers thick. Outside the longitudinal muscle is the circular muscle (CM), six to seven fibers thick.

Neoxabea bipunctata DeGeer

In this species the proventriculus is of the same size and structure as that of *O. nigricornis*.

Trigonidiinae

Falcicula hebardi Rehn

In this species each longitudinal fold in the globular part of the proventriculus is 0.3 mm. long and 0.2 mm. wide (Fig. 33). Each fold bears four appendages. The median tooth (MT) is bifurcated and bears a few irregular median denticles (MD). The lateral tooth (LT) extends from the central part of the median tooth laterally and then posteriorly to well beyond the posterior extremity of the median tooth. It bears sharp spines projecting posteriorly. The inner barbated lobe (IBL) is rounded, and the outer barbated lobe (OBL) bears short, blunt spines. The partition (CP) is co-extensive with the series of four appendages.

Anaxipha exigua Say

The globular part of the proventriculus is 0.5 mm. long and each longitudinal fold is 0.25 mm. wide and bears six appendages, the structure of which is the same as in *Falcicula hebardi*.

Phyllopalpus pulchellus Uhler

The globular part of the proventriculus is 0.6 mm. long and each longitudinal fold bears nine appendages, the structure of which is the same as in *Falcicula hebardi*, except that the posterior branches of the lateral teeth (Fig. 34—LT) do not extend beyond the median tooth.

Cyrtoxiphia columbiana Caudell

The globular part of the proventriculus is 0.5 mm. long and each longitudinal fold bears six appendages. The structure of these is the same as in *Falcicula hebardi* except that the lateral teeth (Fig. 35—LT) do not extend beyond the median tooth.

*Eneopterinae**Hapithus brevipennis* Saussure

The proventriculus is 5 mm. long. Each of the six longitudinal folds in the globular part is 2.5 mm. long and has 12 to 13 appendages. The anterior appendage on each fold is 0.6 mm. wide and the others are progressively smaller toward the last one, which is 0.3 mm. wide. On each appendage the median tooth (Fig. 42—MT) has a long posterior projection bearing six to eight median denticles (MD). The lateral denticles (LD) are short and have a few short serrations. The lateral teeth (LT) extend posteriorly slightly beyond the extremities of the lateral denticles. The inner barbed lobe (IBL) is rounded and bears hairs, and the outer barbed lobe (OBL) has a flat surface toward the lumen of the proventriculus.

Orocharis saltator Uhler

The proventriculus is similar in form to that of *Hapithus brevipennis* but is slightly less than one half its size.

Tafalisca lurida F. Walker

The proventriculus is 3 mm. long and each fold in the globular part is 1.5 mm. long. The form of the appendages is the same as in *H. brevipennis* and *O. saltator* except that the posterior projection of the median tooth (Fig. 43—MT) is only half as long as in these two species.

*Nemobiinae**Nemobius fasciatus* DeGeer

The proventriculus is 3 mm. long and each longitudinal fold in the globular part is 1 mm. long. Some of the lobes in the neck bear a few spines projecting posteriorly. Each longitudinal fold in the globular part bears nine appendages. The anterior appendage on each fold is 0.3 mm. wide and the others are progressively smaller toward the posterior one, which is 0.15 mm. wide. In each appendage the median tooth (Fig. 38—MT) has a posterior

projection with roughly parallel borders bearing three or four short median denticles (MD). The lateral teeth (LT) have rounded lobes. The lateral denticles (LD) are truncated and concave at their extremities. The inner barbated lobes (IBL) are rounded and beset with hairs.

Gryllinae

Gryllulus domesticus Linnaeus

The proventriculus is 4 mm. long. In the neck some of the lobes bear a few spines projecting posteriorly. Each longitudinal fold in the globular part has 11 appendages, the anterior one being 0.5 mm. wide and the posterior one 0.25 mm. wide. The median tooth (Fig. 39—MT) has a posterior projection with six rounded median denticles (MD). Each lateral denticle consists of a single rounded lobe (LD). The lateral tooth (LT) has several rounded projections. The inner barbated lobe (IBL) is broad and has bristles along its posterior border.

Gryllulus assimilis Fabricius

The proventriculus in this species is similar in size and structure to that of *Gryllulus domesticus*.

A longitudinal section of a short portion of the neck and the globular part of the proventriculus is shown in Fig. 36. It is taken through the mid-line of the median teeth (MT) of opposing longitudinal folds. The inner layer is composed of intima (I) which is thinnest (30 to 50 μ) in the neck (N) and thickest (50 to 75 μ) on the median denticles (MD). Beneath the intima is the epithelial layer (EP) composed of small, roughly cubical cells. This layer projects into the hollows of the appendages and is continuous with the epithelial layer of the gastric caeca (GC) of the mid-gut. Next to the epithelium is the longitudinal muscle (LM). This is most extensive in the appendages where it runs obliquely between the epithelium and the circular muscle. The circular muscle (CM) is six to seven fibers in width at the anterior and posterior ends of the proventriculus and 10 to 12 fibers at the widest part of the proventriculus. The oesophageal valve (Oes. V.) constricts the lumen of the proventriculus at its posterior end and projects into the mid-gut between the gastric caeca.

Miogryllus verticalis Serville

In this species the structure of the proventriculus is similar to that of *G. assimilis* and *G. domesticus* but it is shorter. The length of the whole proventriculus is 2 mm., the length of each longitudinal fold in the globular part is 1 mm., and the number of appendages in each fold is nine.

Anurogryllus muticus DeGeer

The proventriculus is 3.5 mm. long and each longitudinal fold is 2 mm. long and bears 13 appendages, the anterior one of which is 0.5 mm. wide and the posterior 0.25 mm. The form of each appendage differs considerably from the similar structure in *G. assimilis* and *G. domesticus*. The median tooth (Fig. 47—MT) extends posteriorly in a long projection that bears

10 or 12 sharp median denticles (MD). The lateral denticles (LD) and lateral teeth (LT) have several rounded spines at their outer borders. The inner barbated lobes (IBL) extend posteriorly beyond the lateral denticles and bear bristles.

Mogoplistinae

Cycloptilum squamosum Scudder

The proventriculus is 1.5 mm. long and each longitudinal fold is 0.7 mm. long and bears eight appendages. The median tooth (Fig. 44—MT) has a short projection posteriorly with three to five median denticles (MD). The lateral denticles (LD) are short and have several rounded spines. The lateral teeth (LT) project beyond the lateral denticles and have several rounded spines. The inner barbated lobes (IBL) are rounded and bear bristles. The outer barbated lobes (OBL) are roughly triangular. At either side of a longitudinal fold is a partition (CP) that is slightly swollen at its posterior end and has short, scalelike projections. At the posterior end of each longitudinal fold is the round flap of the oesophageal valve (Oes. V.), which bears bristles at its anterior end.

Myrmecophilinae

Myrmecophila oregonensis Brunner

This species has the smallest proventriculus of any studied in the Gryllidae. Its total length is 1 mm. and the length of the longitudinal folds in the globular part is 0.25 mm. Each fold bears five appendages, the first of which is 0.1 mm. wide and the last 0.05 mm. wide. Each appendage is less complicated than are comparable structures in other Gryllidae studied. There is no posterior projection of the median tooth (Fig. 45—MT). The lateral denticles (LD) are represented by small lobes, and the lateral teeth by a series of blunt projections at each side of the appendage (LT). There are no inner barbated lobes. The outer barbated lobes (OBL) are irregular in shape and are progressively smaller toward the posterior lobe. Following the longitudinal fold is the flap of the oesophageal valve (Oes. V.). At either side of each longitudinal fold and coextensive with it is a partition (CP) that continues further parallel with the oesophageal valve. It bears small scales in the region of the anterior part of the oesophageal valve.

GRYLLOTALPIDAE

Scapteriscus vicinus Scudder

The proventriculus is 5 mm. long and each longitudinal fold in the globular part of the proventriculus is 2 mm. long. Between the neck and the globular part on each longitudinal fold there is a cushion (Fig. 41—CC) bearing hairs. Each longitudinal fold bears 12 to 13 appendages. The anterior one is 0.5 mm. wide and the posterior one 0.25 mm. wide. The median tooth has no posterior projection but bears a row of blunt median denticles (Fig. 37—MD). The lateral denticles (LD) are truncated and concave at their margins. The lateral teeth (LT) are broad at the tip. The

inner barbated lobes (IBL) are pointed and beset with bristles. The outer barbated lobes (Fig. 41—OBL) are roughly square at the base and extend irregular projections into the lumen. The partitions (CP) are parallel to the longitudinal folds and have small scalelike projections.

Gryllotalpa hexadactyla Perty

The proventriculus is 6 mm. long and each longitudinal fold in the globular part is 3 mm. long and bears 14 appendages. The structure of these appendages is the same as in *S. vicinus* except that there is only a single median denticle (Fig. 47—MD) in the form of a short tubercle.

Terms Used by Authors in Describing the Proventriculus of Grylloidea

Median tooth:

- small median tooth (Berlese)
- median point of median tooth (Bordas)
- median tooth (DuPorte)

Median denticles:

- median denticles (DuPorte)

Lateral tooth:

- small internal tooth (Berlese)
- lateral points of median tooth (Bordas)
- lateral tooth (DuPorte)

Lateral denticles:

- lateral points of median tooth (Bordas)
- lateral denticles of median tooth (DuPorte)

Inner barbated lobe:

- small external tooth (Berlese)
- lateral lobe of median tooth (Bordas)
- inner barbated lobe (DuPorte)

Outer barbated lobe:

- lateral tooth (Bordas)
- outer barbated lobe (DuPorte)

Sclerotized partition:

- chitinous line (Berlese)
- chitinous partition (Bordas, DuPorte)

TETTIGONIOIDEA

Historical Note

Mulder (82) figured a lateral view of the digestive tract of a "Locustid" but gave no details of the internal structure of the proventriculus.

The structure of the proventriculus of the common European insect *Tettigonia verrucivora* Linnaeus (*Decticus verrucivorus* Linnaeus) has been described

by Graber (54) and Wilde (119). The structure of the proventriculus of *Phasgonura viridissima* (*Locusta viridissima*) Linnaeus has been investigated by Wilde (119) and Ramme (92). Other European species in which the proventriculi have been studied are *Conocephalus fuscus* (Fabricius) = *Xyphidium fuscum* Fabricius (Graber, 54), *Ephippiger ephippiger* Fiebig (*E. vitium* Serville) (Graber, 54), and *Meconema varia* Fabricius (Wilde, 119).

Bordas (16) described briefly the proventriculus of several species of the "Locustidae" in his comparative studies of the digestive tract of orthopteroid insects. Davis (37) investigated the structure of the proventriculus of the large tettigoniid *Stenopelmatus fuscus* Haldemann.

Snodgrass (104) studied the external features of the digestive tract of *Peranabrus scabricollis* (Thomas) but gave no details on the internal structure of the proventriculus.

Original Descriptions

TETTIGONIIDAE

Copiphorinae

Neoconocephalus ensiger Harris

The body of the globular part of the proventriculus is 2 mm. long (Fig. 5—P) and it is joined to the crop (C) by a tubular neck (N). Where it joins the mid-gut (MG) it is embedded between two bulbous gastric caeca (GC). In the neck there are six longitudinal rows of cushions covered with hairs (Fig. 48—C) with 8 to 12 cushions in each row. The anterior cushions are small and bear few hairs while the posterior cushions are broad and bear a heavy coat of hairs. All but the last four cushions in each row bear a pointed projection (CT) that extends posteriorly and has sharp spines on its surface. Between each two rows of cushions in the neck there is a series of folds in the form of a double loop (CH) covered with hairs. Each of the six longitudinal folds in the globular part of the proventriculus has 12 appendages (T). The anterior one is 0.8 mm. wide and the size of the others decreases regularly toward the posterior one, which is 0.3 mm. wide. Each appendage has a median tooth (MT), which projects into the lumen of the proventriculus and has a serrated posterior border. From the side of the median tooth there extends to each side a lateral lobe (LL). At each side of the appendage there is a barbed lobe (BL) roughly triangular at the base and with a blunt point projecting posteriorly. Between the longitudinal folds and coextensive with them there is a partition (CP), the surface of which is covered with scale-like projections. At the posterior end of each longitudinal fold there is a flap of the oesophageal valve (Oes. V.) roughly triangular and beset with hairs at its anterior end.

Transverse section (through appendages Fig. 49).—The inner layer is the intima (I), which is thickest (30 to 40 μ) over the median teeth (MT) and the lateral lobes (LL). Beneath this is the epithelial layer (EP), which is composed of rounded or cubical cells and extends into the cavities of the median teeth, barbed lobes (BL), and partitions (CP). The longitudinal muscle

(LM) is one to three fibers thick and the circular muscle (CM) 10 to 12 fibers thick.

Belocephalus subapterus subapterus Scudder

Bucrates malivolans Scudder

Pyrgocorypha uncinata Harris

The proventriculus of these species is the same in size and structure as that of *N. ensiger*.

Conocephalinae

Conocephalus fasciatus DeGeer

The proventriculus is 2 mm. long and each longitudinal fold in the globular part of the proventriculus is 0.8 mm. long and bears nine appendages (Fig. 50—T). The structure of the proventriculus is similar to that of *N. ensiger*.

Transverse sections (Fig. 51—through the neck of the proventriculus; Fig. 53—through a median tooth; Fig. 52—through the oesophageal valve).—The intima (I) is thinnest (5 to 10 μ) in the neck and oesophageal valve and thickest (25 to 30 μ) on the median teeth (MT) and lateral lobes (LL). The epithelial layer (EP) is one cell thick in the neck and oesophageal valve and two to three cells thick in the cavities of the median teeth and barbed lobes (BL). The longitudinal muscle (LM) is one to three fibers thick and the circular muscle four to five fibers thick in the neck and oesophageal valve and six to eight in the globular part of the proventriculus.

Orchelimum gladiator Brunner

The proventriculus is similar in structure to that of *C. fasciatus* but is slightly larger. Its total length is 2.5 mm. and each longitudinal fold bears 11 appendages.

Odontoxiphidium apterum Morse

The proventriculus is similar in size and structure to that of *O. gladiator*.

Phasgonurinae

Phasgonura cantans Fuessly

The proventriculus is similar in size and structure to that of *Neoconocephalus ensiger*.

Decticinae

Atlanticus gibbosus Scudder

In this species the proventriculus has the same general structure as in the Copiphorinae, Conocephalinae, and Phasgonurinae. It is 5 mm. long and each longitudinal fold in the globular part is 2 mm. long. In the neck are the cushions (Fig. 54—C) bearing hairs, the serrated projections (CT), and the loop of hairs (CH). Each longitudinal fold has 18 appendages. The anterior appendage is 0.5 mm. wide and has a heavy armature, and the size of the other appendages decreases regularly toward the posterior one, which is 0.3 mm. wide and has a much weaker armature. The surface of an appendage

is covered with short spines (Fig. 55). The median tooth (MT) projects posteriorly and a shorter lateral projection (LP) extends laterally at each side. There is a smooth lateral lobe (LL) extending from each side of the base of the appendage. At each side of an appendage is the barbed lobe (Fig. 54—BL). The sclerotized partitions (CP) extend parallel to the longitudinal folds and are 0.1 mm. wide. A flap of the oesophageal valve (Oes. V.) extends posteriorly from the end of each longitudinal fold.

Pholidoptera griseoaptera DeGeer

The proventriculus is similar in structure to that of *A. gibbosus* except that the spines covering the appendages are rounded rather than sharp (Fig. 56). The organ is 2.5 mm. long and each longitudinal fold in the globular part is 1.5 mm. long and bears 14 appendages.

Chelidoptera albopunctata Goeze

The proventriculus is 2.5 mm. long and each longitudinal fold is 1.5 mm. long and bears 14 appendages. The structure is the same as in *A. gibbosus* except that the spines on the surface of the appendages are two or three times larger (Fig. 57).

Eremopedes balli Caudell

The proventriculus is the same in all respects to that of *C. albopunctata* except that it is slightly larger, its total length being 3 mm., and the length of each longitudinal fold being 2 mm.

Neduba carinata Walker

The proventriculus is 3 mm. long and each longitudinal fold is 1.5 mm. long. Its structure is the same as in *A. gibbosus* except in the form of the appendages in which the median tooth (Fig. 58—MT) extends backward as a blunt spine bearing irregular tubercles. The lateral projections (LP) are blunt and rounded and the lateral lobes are pointed (LL).

Anabrus simplex Haldemann

The proventriculus is 5 mm. long and each longitudinal fold is 2.5 mm. long and bears 15 appendages in which the median teeth (Fig. 59—MT) and the spines on the surface are rounded, short, and scalelike.

Pediocetes haldemanni Girard

This species has the largest proventriculus of all the Decticinae studied. It is 6 mm. long and each longitudinal fold is 3 mm. long and bears 18 appendages. The surface of each appendage is covered with coarse, sharply pointed spines of irregular length (Fig. 60).

Phaneropterinae

Scudderia curvicauda DeGeer

The proventriculus in this species is similar to that of other species in the Tettigoniidae except that its inner lining has a much less robust armature. It is 3 mm. long and each longitudinal fold in the globular part is 1.5 mm. long. In the neck are the longitudinal rows of cushions bearing hairs (Fig. 69—CH)

and the lobes (CT) are serrated at their tips. On each longitudinal fold of the globular part there are 18 appendages. Each appendage has a median tooth (MT) with a serrated posterior border, and a narrow lateral lobe (LL) projecting laterally from each side of the appendage. The whole surface of the appendage except the median tooth is thickly clothed with hairs and fine spines (CS). In the posterior six or seven appendages the median tooth is replaced by a tuft of hairs. The barbed lobes (BL) at each side of each appendage have a small spine surrounded by a tuft of hairs. The partitions (CP) run parallel to the longitudinal fold at the end of which is the round flap of the oesophageal valve (Oes. V.).

Transverse sections (through posterior part of neck—Fig. 67, through median tooth of appendage—Fig. 68).—The intima (I) is 20 to 25 μ thick over the lateral lobes (LL) and partition (CP) and 5 to 10 μ thick over the remaining surfaces such as the barbed lobes (BL). The epithelial layer (EP) is one cell in width at the base of the appendages and partitions and three to four cells wide in the cavities of the appendages. The longitudinal muscle (LM) is one fiber in thickness or absent entirely at the base of the appendages and is three to four fibers thick in the appendages. The circular muscle (CM) is six to eight fibers wide.

Arethaea arachnopyga Rehn and Hebard

The structure of the proventriculus is the same as in *Scudderia curvicauda*. It is 2 mm. long and each longitudinal fold in the globular part is 1 mm. long and has 12 appendages.

Montezumina modesta Brunner

The proventriculus is similar in size and structure to that of *Scudderia curvicauda*.

Amblycorypha oblongifolia DeGeer

The proventriculus is similar in size and structure to that of *Scudderia curvicauda*.

Microcentrum rhombifolium Saussure

The proventriculus is similar in size and structure to that of *Scudderia curvicauda*.

Stilpnochlora couloniana Saussure

The proventriculus is similar in structure to that of *Scudderia curvicauda* but is slightly larger, being 4 mm. long.

Insara elegans Scudder

The proventriculus is similar in structure to that of *Scudderia curvicauda* but is only 2 mm. long and has 12 to 13 appendages in each longitudinal fold.

Inscudderia walkeri walkeri Hebard

The proventriculus is similar in size and structure to that of *Scudderia curvicauda*.

STENOPELMATIDAE

Stenopelmatinae

Stenopelmatus fuscus Haldemann

The proventriculus is 3.5 mm. long and each longitudinal fold in the globular part is 1.5 mm. long and bears 11 appendages. It is similar in structure to that in *Neoconocephalus ensiger* Harris but differs slightly in that the median tooth of each appendage is slightly more prominent (Fig. 61—MT).

Henicinae

Hemideina megacephala Buller

The proventriculus is 6 mm. long and each longitudinal fold in the globular part is 4 mm. long and bears 20 to 22 appendages each of which is 0.75 mm. wide. The general structure is similar to that of *Stenopelmatus fuscus* Haldemann but the appendages differ considerably. The median tooth (Fig. 62—MT) has a posterior projection bifurcated at the tip and has small scalelike protuberances on its surface. The lateral lobes (LL) are broad at the tip. The anterior border of the appendage bears hairs.

Cratomelus sp.

The proventriculus is 4 mm. long and each longitudinal fold in the globular part is 2 mm. long and bears 12 appendages. The general structure is similar to that of *Hemideina megacephala* Buller but the appendages are different. The median tooth (Fig. 63—MT) extends posteriorly as a rounded lobe that has a blunt median tip. The lateral lobes (LL) are broad at the tip, and the anterior border of the appendage bears hairs.

PROPHALANGOPSIDAE

Cyphoderris monstrosa Uhler

The proventriculus is 5 mm. long and each longitudinal fold is 2.5 mm. long and bears 12 appendages. The general structure of the proventriculus is the same as in the Copiphorinae and Stenopelmatinae. The median tooth, however, is relatively longer and bears irregular tubercles (Figs. 73, 74—MT). The lateral lobes (LL) are blunt and the surface of the appendage is covered with scalelike protuberances, and the posterior border of the appendage bears hairs.

RHAPHIDOPHORIDAE

Ceuthophilus maculatus Harris

The proventriculus is 3 mm. long and globular (Fig. 6—P) with a neck (N) attached to the posterior end of the crop (C). Where it joins the mid-gut (MG) it is embedded between two bulbous gastric caeca (GC). In the neck are the six longitudinal rows of six to seven cushions (Fig. 66—CC) bearing hairs. Each of the anterior five of these cushions has a roughly rectangular projection (CT) with short spines. Each of the longitudinal folds in the

globular part has 10 or 11 appendages. The median tooth (MT) of each appendage is a tuft of hairs, and a pair of lateral lobes extends outward from the median tooth. The anterior barbated lobes (BL) are roughly square at the base and have a blunt projection toward the lumen of the proventriculus. The posterior barbated lobes are smaller than the anterior and are irregular in shape. Each longitudinal fold is followed by a flap of the oesophageal valve (Oes. V.) and flanked by a partition covered with small scalelike lobes (CP).

Pristoceuthophilus pacificus Thomas

The proventriculus is 2 mm. long and each longitudinal fold in the globular part bears six appendages. The structure is the same as in *Ceuthophilus maculatus* Harris.

Udeopsylla robusta Haldemann

The proventriculus is the same in size and structure as that of *Ceuthophilus maculatus* Harris.

Styracosceles neomexicanus Scudder

The proventriculus is the same in size and structure as that of *Ceuthophilus maculatus* Harris.

Daihinia brevipes Haldemann

The proventriculus is the same in size and structure as that of *Ceuthophilus maculatus* Harris.

Hadenoecus puteanus Scudder

The proventriculus is 3 mm. long and each longitudinal fold is 1.5 mm. long. In the neck there are the cushions (Fig. 28—CC) with their sclerotized lobes (CT). The structure of the appendages in the globular part differs considerably from that in the other Rhipidophoridae studied. The appendages in each longitudinal row are 12 in number, the anterior one being 0.4 mm. wide and the posterior one 0.2 mm. wide. The anterior barbated lobes (BL) are roughly square at the base and bear strong projections extending posteriorly while the posterior ones are much smaller than the anterior and do not bear projections. The partitions (CP) are 0.1 mm. wide anteriorly and taper to a point posteriorly. On an appendage (Fig. 64) there is a blunt median tooth (MT) with short spines. The lateral lobes are short and thick (LL) and the anterior border of each appendage is concave and bears hairs that extend over the appendage toward the lateral lobes.

Tachycines asynamorus Adelung

The proventriculus is similar in size and structure to that of *Hadenoecus puteanus* Scudder except in the structure of the appendages in which the lateral lobes (LL) are subdivided into two smaller lobes (Fig. 65).

Terms Used by Authors in Describing the Proventriculus of Tettigonioidea

Median tooth:

- median tooth (Bordas)
- chitinous tooth (Davis)

Posterior projection of median tooth:

- median lobe (Bordas)
- apical denticle (Davis)

Lateral projection:

- lateral denticle (Bordas, Davis)
- lateral tubercle (Bordas)

Lateral lobe:

- lateral lobe (Bordas)

Barbated lobe:

- lateral tooth (Bordas)
- chitinous tubercle (Bordas)
- barbated lobe (Davis)

Sclerotized partition:

- chitinous partition (Bordas, Davis)

CAELIFERA

ACRIDOIDEA

ACRIDIDAE

Historical Note

Dufour (42) described the proventricular region of *Oedipoda caerulescens*, but regarded the Acrididae as having no "gésier".

Faussek (50) gave a short description of the proventriculus of *Eremobia muricata* Pall.

Visart (110) gave a short description of the proventriculus of *Oedipoda caerulescens* Linnaeus.

Bordas (15) investigated the digestive tract of *Pamphagus elephas* Stal and (16) described briefly the proventricular region of several species of Acrididae.

Tietz (109) described the digestive tract of *Dissosteira carolina* Linnaeus.

Hodge (66, 67, 68) made a detailed investigation of the digestive tract of *Melanoplus differentialis* Thomas, *Locusta migratoria* Linnaeus, and *Rade-notatum carinatum* var. *peninsulare* Rehn and Hebard.

Original Descriptions

*Oedipodinae**Dissosteira carolina* Linnaeus

With the crop (Fig. 7—C) and the mid-gut (MG) the proventriculus (P) forms a tube 1 mm. in diameter. At the level at which the proventriculus

joins the mid-gut there are six gastric caeca (GC) of the mid-gut. Each of these has a tubular anterior portion 4 mm. long and a tubular posterior portion 2 mm. long. The lining of the posterior part of the crop shows about 40 longitudinal ridges (Fig. 70—LR) each of which is 0.1 mm. wide and bears a series of flat scalelike projections (S). Posteriorly the longitudinal ridges converge to form six longitudinal plates (LP) of the proventriculus. Each of these is 1 mm. long and 0.5 mm. broad at its anterior end and tapers slightly toward its rounded posterior border. The surface of each plate bears fine scalelike projections. Between the longitudinal plates there are a few weak irregular folds.

Transverse sections (Fig. 75—through posterior end of crop; Fig. 76—through converging longitudinal ridges; Fig. 77—through anterior ends of the longitudinal plates; Fig. 78—through posterior ends of the longitudinal plates).—The inner layer is the intima (I), 20 to 30 μ thick. The epithelial layer (EP) is one cell in thickness. The longitudinal muscle (LM) is two to four strands thick in the longitudinal plates and is associated with a few transverse muscles (TM). The circular muscle (CM) is three to six fibers thick.

Arphia sulphurea Fabricius

Arphia pseudonietana Thomas

Encoptolophus sordidus Burmeister

Pardalophora apiculata Harris

Hippiscus rugosus Scudder

Spharagemon bolli Scudder

Scirtetica marmorata Harris

Psinidia fenestralis Serville

Trimerotropis pallidipennis Burmeister

Circotettix verruculatus Kirby

In these species the proventriculus is similar in structure to that of *Dissosteira carolina* Linnaeus.

Cyrtacanthacrinae

Dendrotettix quercus Packard

In this species the proventriculus is similar to that of *Dissosteira carolina* Linnaeus, having the longitudinal ridges (Fig. 71—LR) and scalelike projections (S) in the crop, and the longitudinal plates (LP) of the proventriculus. The lining is, however, more robust, with stronger scalelike projections in the crop and relatively more scalelike projections on the longitudinal plates of the proventriculus.

Gymnoscirtetes pusillus Scudder

Campylacantha olivacea olivacea Scudder

Hesperotettix festivus Scudder

Podisma pedestris Linnaeus

Aptenopedes sphenarioides apalachee Hebard

Paroxya clavuliger Serville

Melanoplus bivittatus Say

Melanoplus punctulatus Scudder

Melanoplus femur-rubrum DeGeer

Schistocerca americana Drury

The proventriculus in these species is similar to that of *Dendrotettix quercus* Packard and of *Dissosteira carolina* Linnaeus, some being relatively more robust as in the former and some less robust as in the latter, depending upon the size.

Romaleinae

Romalea microptera Beauvais

The proventriculus is similar in structure to that of *Dendrotettix quercus* Packard but in keeping with the size of the insect it is twice as big, the longitudinal plates being 4 mm. long.

Acridinae

Chloealtis conspersa Harris

The proventriculus is similar in size and structure to that of *Dissosteira carolina* Linnaeus and *Dendrotettix quercus* Packard and shows the longitudinal ridges (Fig. 72—LR) and fine scalelike projections (S) of the crop and the longitudinal plates of the proventriculus (LP). It is, however, less robust than that in the aforementioned species, having very fine scales (S) in the crop and comparatively fewer scales on the longitudinal plates.

Syrbula admirabilis Uhler

Eritettix simplex tricarinatus Thomas

Amphitornus coloradus ornatus Scudder

Amblytropidia occidentalis Saussure

Orphulella pelidna Burmeister

Dichromorpha viridis Scudder

Clinocephalus elegans Morse

Chorthippus curtipennis Harris

Ageneotettix deorum Scudder

In these species the proventriculus is similar in structure to that of *Chloealtis conspersa* Harris.

In all the species of Acrididae investigated the proventriculus shows a common form throughout, any differences being in the relative robustness of the structures. In the larger forms such as *Romalea microptera* Beauvais the longitudinal plates are large and bear many scalelike projections while in smaller forms such as *Chloealtis conspersa* Harris the plates are small and less heavily sclerotized and bear fewer scalelike projections.

Terms Used by Authors in Describing the Proventriculus of Acrididae

Longitudinal ridge of crop:

—longitudinal fold (Bordas)

—longitudinal ridge (Dufour, Hodge)

Longitudinal plate of proventriculus:

- chitinous plate (Bordas)
- tooth of gizzard (Dufour)
- arrow-shaped plate (Faussek)
- proventricular tooth (Hodge, 1936)
- proventricular plate (Hodge, 1940)

TETRIGIDAE

Historical Note

Carpentier (27) described the external features of the alimentary canal of *Acrydium Kiefferi* but gave no details on the internal structure.

Original Descriptions

*Batrachidinae**Tettigidea lateralis parvipennis* Harris

Externally the proventriculus (Fig. 9—P) is a tubular structure continuous with the crop (C) and entering the mid-gut (MG) between the bases of the six gastric caeca (GC). The caeca project forward from the anterior end of the mid-gut and are about 1 mm. long. The lining of the proventriculus is a thin intima with a few weak longitudinal folds posteriorly.

Longitudinal section (Fig. 79).—The inner lining of the crop and proventriculus is the very thin intima (I), which consists of an inner layer 2 to 3 μ thick and an outer layer 5 to 10 μ thick. The epithelial layer (EP) is one cell thick and continuous with the epithelial layer of the gastric caeca (GC) and oesophageal valve (Oes. V.). The circular muscle (CM) is present as a few scattered fibers in the crop and is two to three fibers thick in the proventriculus and oesophageal valve.

*Tetriginae**Paratettix cucullatus* Burmeister

The proventriculus is similar to that of *Tettigidea lateralis*. Its lining is uniformly smooth and posteriorly shows six longitudinal folds that are weakly defined (Fig. 80—LF).

TRIDACTYLOIDEA

TRIDACTYLIDAE

Historical Note

Carpentier (27) described the external features of the digestive tract of *Tridactylus thoracicus* Guérin.

Original Description

Tridactylus apicalis Say

The proventriculus (Fig. 10—P) forms a tubular structure with the crop (C) and enters the mid-gut (MG) between two bulbous gastric caeca (GC). These gastric caeca project forward from the anterior end of the mid-gut and

are about 0.5 mm. long. The inner lining of the proventriculus (Fig. 82—I) is thin and continuous with that of the crop (C) and shows a few weak longitudinal ridges where it constricts to form the oesophageal valve.

Transverse section (Fig. 83).—The proventriculus lies between the two gastric caeca (GC). Its inner lining is the intima (I), 2 to 5 μ thick and raised in irregular longitudinal folds. The epithelial layer (EP) is composed of a single layer of cells. The circular muscle (CM) is three to four fibers thick.

CYLINDRACHAETIDAE

Historical Note

Carpentier (27) described the external features of the digestive tract of *Cylindrorcytes spegazzini* but gave no details on the internal structure.

Original Description

Cylindrorcytes spegazzini Giglio-Tos

The crop (Fig. 8—C) and proventriculus (P) are tubular and enter the mid-gut (MG) between the bases of the six gastric caeca (GC). These gastric caeca project forward from the anterior end of the mid-gut and are 2 mm. long. The lining of the proventriculus (Fig. 81—P), in common with that of the crop (C), is uniformly smooth and unrelieved by any projections. As it narrows toward the oesophageal valve (Oes. V.) the lining forms weak transverse furrows.

G R Y L L O B L A T T A R I A

GRYLLOBLATTIDAE

Original Description

Grylloblatta campodeiformis Walker

The proventriculus consists of a globular body (Fig. 11—P) and a tubular neck (N) joined to the crop (C). The globular body enters the mid-gut (MG) between two short gastric caeca (GC). The lining of the neck and anterior part of the body of the proventriculus shows 12 longitudinal primary folds (Fig. 85—PF), which bear an armature of fine scalelike points (S). In the posterior half of the body of the proventriculus the primary folds alternate with, and at the posterior border are replaced by, 12 secondary folds (SF), which likewise bear the armature of fine points. At the posterior end of the proventriculus there are two ranks of pyramidal teeth, which project into the lumen of the proventriculus. They bear a coat of fine hairs. The teeth in the primary rank (PT1) are 0.3 mm. long and are borne at the posterior ends of the 12 secondary folds. The teeth in the secondary rank (PT2) are 0.4 mm. long and are borne at the posterior ends of the primary folds. Posterior to the ranks of teeth is the lining of the oesophageal valve (Oes. V.).

Longitudinal section (Fig. 88) and *transverse sections* (Fig. 86—through primary folds; Fig. 87—through primary and secondary folds; Fig. 89—through

primary and secondary ranks of teeth; Fig. 90—through one primary tooth and two secondary teeth; Fig. 91—through secondary rank of teeth; Fig. 92—through single secondary tooth).—The intima (I) is 10 to 15 μ thick and bears the fine scalelike points. The epithelial layer (EP) is one to four cells thick and is continuous with that of the oesophageal valve (Oes. V.) and gastric caeca (GC). The longitudinal muscle (LM) is sparse except in the pyramidal teeth (PT) where it is several fibers thick. The circular muscle (CM) is three to four fibers thick in the neck region and 8 to 10 fibers thick in the globular part.

ISOPTERA

Historical Note

Sutherland (107) studied longitudinal sections of the alimentary canals of species in six genera of Isoptera.

Original Description

TERMITIDAE

Calotermitinae

Termopsis angusticollis Hagen (worker)

The proventriculus is conical and 1 mm. long. In its anterior end are 12 teeth (Fig. 84—CT). These are narrow and have a thin plate projecting into the lumen of the proventriculus. This plate is tallest and most heavily sclerotized at the anterior end of the tooth. At each side of each tooth there is a narrow longitudinal fold (LF). Posterior to each of six alternate teeth is a large cushion (C), rounded at its anterior end, bearing small rounded tubercles, and tapering posteriorly to the oesophageal valve (Oes. V.).

Terms Used by Authors in Describing the Proventriculus of Isoptera

Sclerotized tooth:

—narrow fold (Sutherland)

Cushion:

—lower cushionlike fold (Sutherland)

DERMAPTERA

Historical Note

Bordas (9, 16) described the proventriculus of *Forficula auricularia* Linnaeus.

Original Description

LABIDURIDAE

Anisolabis maritima Buller

The proventriculus (Fig. 97—P) is a tubular structure 1.5 mm. long with its anterior end widened slightly to join the crop (C). The tubular posterior end enters the mid-gut (MG).

On the inner surface of the proventriculus the intima has six longitudinal folds (Fig. 98—LF). At its anterior end each fold bears an oval cushion (CC) projecting into the lumen and clothed with sharp bristles. The remainder of the surface of the fold is covered with rounded scalelike projections. At the posterior end of each fold is a slight constriction followed by a conical flap of the oesophageal valve (Oes. V.). This flap bears sharp bristles similar to those on the cushion at the anterior end of the longitudinal fold.

Terms Used by Authors in Describing the Proventriculus of Dermaptera

Longitudinal fold:

—spatulate strip (Bordas)

P L E C O P T E R A

Historical Note

Wu (121) described the proventriculus of *Nemoura vallicularia*.

Original Description

PERLIDAE

Acroneuria abnormis (Newman) nymph

In the nymph of this insect the proventriculus is cylindrical (Fig. 12—P) and is continuous with the crop (C). It is surrounded by seven gastric caeca (GC) of the mid-gut (MG) that project forward. Of these the two lateral ones are longest, being 5 mm. long. The other five are 3 mm. long, three being ventral and two dorsal.

The proventriculus is 0.3 mm. long. The anterior part of the intima of the organ is traversed by 14 longitudinal plates beset with small spines (Fig. 93, Fig. 94—LT). Posteriorly these anastomose to form 12 plates in the posterior part of the proventriculus (Fig. 96—LT). Six of these project farther into the lumen of the proventriculus than do the six that alternate with them. Beneath the intima is a layer of small epithelial cells (Figs. 95, 96—EP). In the cavities beneath the plates are strands of longitudinal muscle (Figs. 95, 96—LM). The outer wall of the proventriculus consists of circular muscle three to four strands thick (Figs. 95, 96—CM).

Discussion

For sound phylogenetic studies it is necessary to take into account the total structure of the organisms investigated. The earlier workers on insects in this field concerned themselves mainly with the details of the external structures such as the venation of the wings and the modifications of the mouth parts. This work was carried further, in the study of orthopteroid insects, by investigation of such structures as the terminal abdominal appendages, as noted in the "Historical Review". A pioneer in the study of internal anatomy for comparative purposes was Bordas who worked on the features of the digestive tract (14, 16) and of the nervous system (18).

Internal structures have not been used extensively in taxonomic and phylogenetic studies largely because of the difficulty of dissecting them out and preparing them for study. As a result of this neglect some insects have been assigned to taxonomic groups after their external features alone have been studied, whereas investigation of the details of their internal anatomy have indicated that they should be included in some other taxonomic group. This will be most clearly illustrated later in consideration of the phylogenetic relationships of the 'sand-cricket', *Tridactylus apicalis* Say. This is an insect of fossorial habit, which bears a superficial resemblance to the 'mole-crickets' and which has therefore been assigned to the Ensifera. Closer study of the details of both external and internal anatomy indicates that it should be assigned to the Caelifera.

As indicated in the "Historical Review" several authors have based their phylogenetic schemes upon investigations of the fossil record. Remains and impressions of internal structures are lacking in fossils, and consequently deductions concerning phylogeny based upon internal characters can be made only from the study of insects now existing. The existence, in the past, of ancestral groups of orthopteroid insects, such as "Protobattoidea" and "Protorthoptera" is deduced mainly from the study of fossils and of the external characters of insects now existing.

For purposes of comparison reference may be made to diagrams illustrating the phylogenetic schemes of various authors: Walker (112), Crampton (35), Handlirsch (in Schröder (101), 1925), Karny (75) (in Ander (1)), Ander (1, 2), Zeuner (122).

BLATTODEA

In the cockroaches investigated in this study the proventriculus is conical, with the crop joining the cone at its broad base, and with the apex of the cone entering the mid-gut as an oesophageal valve surrounded by the eight tubular gastric caeca of the mid-gut. The structure of the intima likewise shows a common pattern. The anterior portion is occupied by six sclerotized teeth alternating with varying numbers of folds or spine-bearing patches. Posterior to each tooth there are one or two cushions followed by the oesophageal valve.

MANTODEA

In all the species of mantids investigated the proventriculus shows a common structure. It is conical in shape with the broad end of the cone leading from the crop, and the apex of the cone entering the mid-gut as the oesophageal valve. At the anterior end of the mid-gut are eight tubular gastric caeca immediately posterior to the proventriculus. The anterior portion of the inner lining of the proventriculus is occupied by six teeth running longitudinally, and by six areas of anastomosing ridges alternating with the teeth.

Posterior to each tooth there are two cushions followed by the oesophageal valve. In the species of the four subfamilies studied there are no evident differences of structure by which to separate the subfamilies one from another.

The gross structure of the proventriculus of the Mantodea is very similar to that of the Blattodea and differs only in that there are areas of anastomosing ridges between the teeth of the former rather than series of longitudinal folds as in the latter. This similarity of structure leads to the conclusion that the Mantodea and Blattodea are closely related, a conclusion amply supported by the work of various authors on other structures: Bordas (14, 16)—alimentary canal; Bordas (18)—nervous system; Walker (111, 112)—terminal abdominal appendages; Crampton (29, 35)—external characters; Ford (53)—abdominal musculature; Handlirsch (57) and Zeuner (122)—fossil record; Nesbitt (83)—nervous system. The common ancestry of the two orders is shown in their being assigned by Handlirsch (in Zeuner, 122) to a superorder Blattaeformia derived from the "Protoblattoidea".

ISOPTERA

In the form studied in this order, *Termopsis angusticollis* Hagen, the proventriculus is similar to that of the Blattodea and Mantodea. It is conical, and adjacent to its posterior end are eight tubular gastric caeca of the mid-gut. Its inner lining resembles more closely that of the Blattodea than of the Mantodea as it has longitudinal folds rather than anastomosing ridges between the teeth. It differs, however, from both orders in having 12 rather than six teeth in its anterior portion.

The work of Sutherland (107) on six other genera of termites indicates that they are closely related to the Blattodea. She studied longitudinal sections of the whole digestive tracts and her figures are similar to that of the writer's figure of *Parcoblatta pennsylvanica* DeGeer (Fig. 14), showing the conical form of the proventriculus, the teeth, and the cushions posterior to the teeth. The close relationship of the Isoptera to the Blattodea and Mantodea is agreed to by several authors: Walker (111, 112)—terminal abdominal appendages; Crampton (35)—external characters; Handlirsch (57) and Zeuner (122)—fossil record; Nesbitt (83)—nervous system; Rau (93)—habits and oviposition. The three orders are assigned to a common superorder "Blattaeformia" by Handlirsch (in Zeuner (122)).

ORTHOPTERA

ENSIFERA

GRYLLOIDEA

In the Grylloidea the globular body of the proventriculus is joined to the crop by a tubular neck and lies between the two bulbous gastric caeca. Internally

the neck bears six longitudinal rows of cushions with hairs, and the globular part has six corresponding longitudinal folds bearing a series of appendages. A well-developed appendage is composed of a median tooth with median denticles, two lateral teeth, two lateral denticles, and two inner barbated lobes. At each side of an appendage there is an outer barbated lobe and each longitudinal fold is flanked by a partition coextensive with it. A flap of the oesophageal valve is situated at the end of each longitudinal fold.

Within the Grylloidea the two families Grylloidae and Gryllidae show differences in structure that are characteristic. In the Grylloidae there is no median posterior projection of the median tooth and the median denticles are represented by either a single tubercle (*Gryllotalpa*) or a row of short median denticles (*Scapteriscus*). In the Gryllidae there is a posterior projection of the median tooth with several median denticles.

TETTIGONIOIDEA

In this group the proventriculus is similar to that of the Grylloidea in consisting of a globular body lying between the two bulbous gastric caeca and a tubular neck joining the body to the crop. Internally there are six longitudinal rows of cushions in the neck and six longitudinal folds, bearing appendages, in the globular part. Each appendage is flanked by a barbated lobe at each side, and each longitudinal fold by a partition. The structure of the appendages, however, differs from that in the Grylloidea in being less complicated. Each well developed appendage consists of a median tooth sometimes with lateral projections, and two lateral lobes. The lateral teeth and inner barbated lobes, present in the Grylloidea, are not present in the Tettigonioidea.

That the Tettigonioidea and the Grylloidea are closely related is a conclusion reached by many authors: Bordas (16)—digestive tract; Bordas (18)—nervous system; Walker (111, 112)—terminal abdominal appendages; Crampston (35)—external features; Handlirsch (57) and Zeuner (122)—fossil record; Ander (1)—external features; Nesbitt (83)—nervous system.

Within the superfamily Tettigonioidea the proventriculus shows considerable variety of structure. The five subfamilies of the Tettigoniidae studied may be divided into two groups on the basis of the structure of the proventriculus: I. Phaneropterinae—in this subfamily the appendages are covered with hairs and the barbated lobes have a small spine surrounded by a tuft of hairs; II. Phasgonurinae, Copiphorinae, Conocephalinae, Decticinae—the appendages have no hairs and the barbated lobes are strong sclerotized structures without hairs.

Considerable difference of opinion exists on the question of the relationships of the groups of 'gryllacrid' insects to one another. One point of view is that of Karny (75) who places all these in a single family Gryllacrididae with

subfamilies Stenopelmatinae, Henicinae, Prophalangopsinae, Deinacridinae, and Rhaphidophorinae. Ander (1), on the other hand, claims that there are several families, e.g. Prophalangopsidae, Rhaphidophoridae, and Stenopelmatidae (subfamilies Stenopelmatinae and Henicinae). The structure of the proventriculus in these insects indicates that the gryllacrids are not a homogeneous group and that Ander's classification indicates the true relationships. In the Rhaphidophoridae the appendages consist of a median tuft of hairs with lightly sclerotized lateral lobes. In the Stenopelmatidae and Prophalangopsidae the appendages are strongly sclerotized and have no median tufts of hairs. They resemble the Tettigoniidae more closely than they do the Rhapidophoridae. Ander (1, 2) sums up this relationship by including the Tettigoniidae, Stenopelmatidae, and Prophalangopsidae in a group "Tettigonaemorpha".

CAELIFERA

In the members of the four families of this group the proventriculus is comparatively simple in structure, being tubular in shape and having no heavy armature on the intima. In the Acrididae the longitudinal folds of the crop converge posteriorly to form six longitudinal plates in the proventriculus, each bearing small scalelike projections. In the Tetrigidae the crop shows no longitudinal folds in its intima, but has six weakly defined longitudinal folds in the proventriculus. In the Tridactylidae and Cylindrachaetidae the thin intima of the crop and proventriculus shows no folds or projections.

The gastric caeca, closely associated with the proventriculus, vary in number and form in the four families. In the Acrididae there are six gastric caeca, each with a long tubular projection forward from its point of attachment to the mid-gut and a shorter tubular projection backward from its point of attachment. In the Tetrigidae and Cylindrachaetidae there are six gastric caeca projecting forward from the mid-gut and there are no posterior projections. In the Tridactylidae there are two gastric caeca projecting forward from the mid-gut and there are no posterior projections.

On the basis of external and internal characters the Acrididae and Tetrigidae are clearly seen to be closely related as members of the suborder Caelifera. In the proventriculus the simple tubular structure prevails in both and both show the six longitudinal posterior folds or plates, better developed in the Acrididae. The work of various authors on other structures confirms this view: Robertson (97)—chromosomes; Walker (111, 112)—terminal abdominal appendages; Ford (53)—abdominal musculature; Carpentier (27)—digestive tract.

The Tridactylidae and Cylindrachaetidae have long been considered as closely related to the Gryllidae and therefore have been assigned to the Ensifera (e.g. Essig (47), Schröder (101, 1929)). This was due to the fact

that these insects are burrowing forms and the legs and body are adapted to fossorial life, and they resemble externally such insects as the fossorial *Gryllotalpa* of the Ensifera. Closer investigation of the external anatomy by Carpentier (25, 26) led to the conclusion that they were allied to the Caelifera, and the study of the external characters of the digestive tract (Carpentier (27)) led to the same conclusion.

The proventriculus is definitely of the type found in the Caelifera and has nothing in common with that of the Ensifera. In *Tridactylus* and *Cylindrocytes* the intima is thin and smooth and unrelieved by any regular folds or projections.

The Caelifera and Ensifera have been assigned to the order Saltatoria (e.g. Handlirsch (57)). Ander (2), however, claims that the Caelifera form "eine selbständige Linie" independent of the Ensifera and (1) that "die beiden Unterordnungen der Saltatoria auf verschiedene Protorthopteren—stammen zurückgehen". The striking difference in the form of the proventriculus and in the form and number of the gastric caeca in the two suborders confirms this view.

PHASMIDA

In the phasmids the proventriculus is a tubular structure continuous with the crop and with the oesophageal valve, which projects as a long flap into the mid-gut. Its only armature on the intima consists of the series of longitudinal folds beset with small spines or scalelike projections.

A difference of opinion on the phylogenetic position of the Phasmida is evident, some authors assigning the group to the Protorthoptera and some to the Protoblattoidea. Ford (53) and Walker (112) consider that the phasmids arise from the base of the stem culminating in the Blattaria and Mantaria, and Nesbitt (83) groups them with the Blattidae and Mantidae on the basis of the number of recurrent nerves. Handlirsch (57), Crampton (35), and Zeuner (122) conclude that the phasmids arise from the Protorthoptera.

The proventriculus of the phasmids does not resemble that of the Ensifera, Acridoidea, or Blattaformia but is considerably less complicated in structure than in these groups, and there are associated with it no well-defined gastric caeca that might give a clue to its relationship with these groups. The simplicity of its structure leads to the conclusion that the Phasmida are primitive types as compared with other orthopteroid insects but it gives no indication of the relationship of the Phasmida to other groups.

GRYLOBLATTARIA

In *Grylloblatta campodeiformis* Walker the proventriculus consists of a globular body and anterior to this a short tubular neck. In the anterior

part of the body the sclerotized intima has 12 longitudinal folds bearing spines, and in the posterior part 12 similar folds that alternate with the posterior ends of those in the anterior part. The part of the proventriculus immediately anterior to the oesophageal valve is occupied by two ranks of pyramidal teeth with 12 teeth in each rank. The globular body of the proventriculus lies between two small gastric caeca.

Since the discovery of this insect by Walker its systematic position has been the subject of much discussion. Crampton (28) assigned the insect to an order Notoptera, and in a later paper (30) concluded that it was related to the Embiids and still later (33) considered that it was related to such forms as the Ensifera. Imms (70) grouped the insect with the "Cursoria", which included the Blattidae and Mantidae. Walker (111, 112, 113, 114, 116, 117) made detailed studies of various structures of *Grylloblatta*. He concluded (116) that it had closer affinities with the Saltatoria such as *Gryllus* than with other groups, but showed considerable resemblance to Plecoptera as represented by *Nemoura vallicularia*. He emphasized (117) the relationship of the Grylloblattaria with the Saltatoria, especially the Ensifera, rather than with the Blattodea, Mantodea, and Isoptera.

The external features of the proventriculus of *Grylloblatta* resemble most closely those of the Ensifera, there being a globular body joined to the crop by a tubular neck. There are, however, no well-developed gastric caeca such as are found in the Ensifera. The anterior end of the mid-gut is invaginated slightly to accommodate the body of the proventriculus and may show two slight projections forward laterally, comparable to the gastric caeca of the Ensifera.

While the proventriculus of *Grylloblatta* does resemble that of the Ensifera in its external appearance it in nowise resembles it in internal structure. The 12 longitudinal folds and the two ranks of pyramidal teeth in the proventriculus of *Grylloblatta* are quite unique. The group that it most resembles is the Plecoptera in that it has the longitudinal folds bearing small spines. But it does not have the tubular shape of the proventriculus of the Plecoptera and there are not the seven gastric caeca as in the mid-gut of the Plecoptera.

The structure of the proventriculus of *Grylloblatta* then, does not indicate close relationship to any of the orthopteroid insects but it suggests that the Grylloblattaria arose from the stem giving rise to the Ensifera.

D E R M A P T E R A

In *Anisolabis maritima* Buller, the proventriculus is a tubular structure with its anterior end flared slightly where it joins the crop. On its inner surface there are six longitudinal folds bearing small scalelike projections with a cushion of bristles at the anterior end of each fold.

The proventriculus in this species does not resemble closely that of any other of the orthopteroid insects studied. However, it is somewhat similar to the proventriculus of the Blattodea. The six cushions bearing bristles are comparable to the ovoid patches of *Pycnoscelus surinamensis* Linnaeus and the longitudinal folds are somewhat comparable to the longitudinal folds leading to the oesophageal valve in several species of Blattodea. But the proventriculus does not have the conical structure of the Blattodea, nor does the mid-gut have the eight tubular gastric caeca characteristic of the Blattodea, Mantodea, and Isoptera.

The phylogenetic position of the Dermaptera has been discussed by several authors. Walker (112) derives the group from the Paleodictyoptera independently of the other orthopteroid groups, but closest to the Plecoptera. Ford (23) says "the arrangement of the muscles also confirms the relationship of the Dermaptera with the Plecoptera". Crampton (35) in his "phylogenetic tree" groups the Dermaptera with the Orthoptera and Phasmids but admits that they have some characters in common with the blattoid insects. Nesbitt (83) groups the Dermaptera with the blattoid insects on the basis of the possession of one posterior recurrent nerve. The structure of the proventriculus does not throw any deciding light on the subject but does indicate that the Dermaptera may be related to the Blattoid insects.

PLECOPTERA

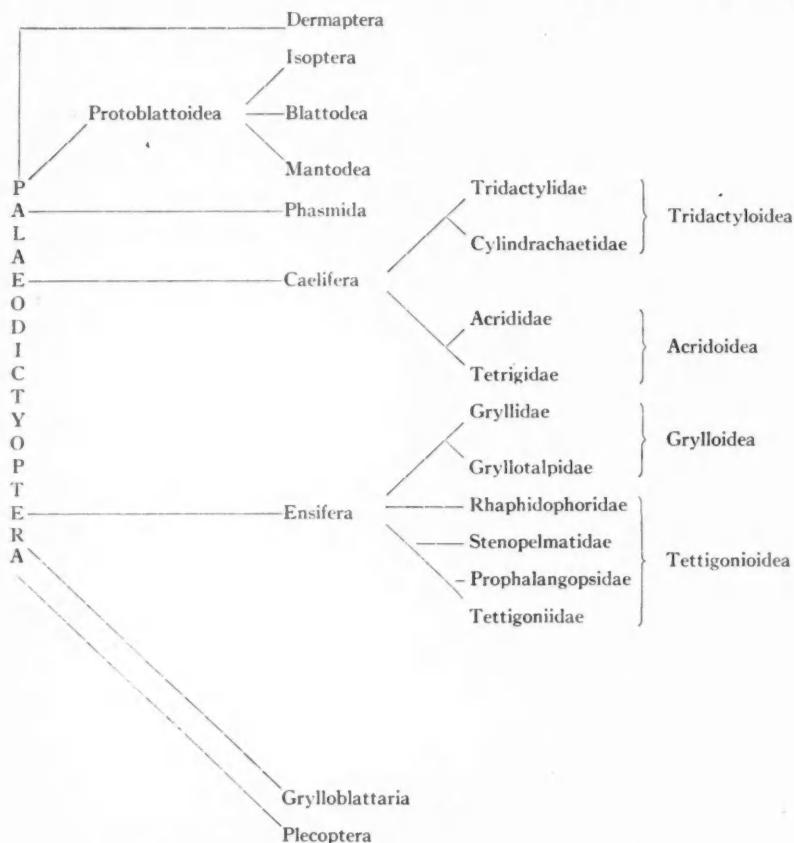
In the form studied in this group, *Acroneuria abnormis*, the proventriculus is tubular and bears on its inner surface 14 longitudinal plates that anastomose posteriorly to form 12 longitudinal ridges. There are seven tubular gastric caeca projecting forward from the mid-gut and surrounding the proventriculus.

The phylogeny of the Plecoptera has been discussed by several authors. Walker (112) derives this group from the Palaeodictyoptera independently of the other orthopteroid insects. Ford (53) says that "the arrangement of the muscles also confirms the relationship of the Dermaptera with the Plecoptera". Crampton (35) considers the Plecoptera to be a group derived from the Palaeodictyoptera independently of the other orthopteroid insects.

The structure of the proventriculus is unlike that of any other of the orthopteroid insects studied except that its inner plates resemble those of *Grylloblatta*, and the presence of seven gastric caeca is unique. On the basis of the structure of this organ, then, it is to be concluded that the Plecoptera form a group independent of the other orthopteroid insects.

Phylogeny

The relationships between the groups of orthopteroid insects arrived at in this study are expressed in the following table:



The "Palaeodictyoptera" is the ancestral form, proposed by Handlirsch (56), from which all winged insects are derived. The main argument for the existence of such a common ancestor for insects is the presence of the two pairs of wings on the same two body segments (mesothorax and metathorax) of all winged insects and the common pattern of the principal veins of the wings.

TAXONOMY

The diversity of structure displayed by the proventriculus of insects has led several authors to base keys for identification of genera on the characters of this organ. Emery (46) composed a "Stammbaum" to show the relationships between genera of the families Dolichoderidae and Camponotidae of ants. Ris (94), basing his results on the structure of the proventriculus of nymphal and adult dragonflies, composed a table to show the relationship of eight families of Odonata to one another. Higgins (64) says of Ris's work

that "classification into genera based on resemblances in gizzard structure would agree in most cases with that now in use based on structure of wings and other external features of the body".

The work of Felt (51) and Swaine (108) on Scolytidae has led these authors to conclude that the proventriculus of these insects is of value in taxonomy; and Swaine says, "I have found the proventriculus of the greatest interest and much practical value; but a wider study is apparently necessary before definite conclusions can be drawn". For the Dytiscidae Balfour-Browne (3) arranged a key, based on the structure of the proventriculus, for the separation of 22 genera; and in another paper (4) he showed that the divisions of Dytiscidae based on the structure of this organ coincided with divisions based on the structure of the tarsal claws. Sutherland (107) concluded that "the alimentary canals of termites of different families can be arranged in a definite series, corresponding to their systematic positions".

The following key, for the forms included in this study, is based upon the external and internal features of the proventriculus and the gastric caeca.

- A. Proventriculus conical, intima with 6 or 12 teeth; eight tubular gastric caeca
 - B. Sclerotized folds between teeth Blattodea, Isoptera
 - BB. Anastomosing ridges between teeth Mantodea
- AA. Proventriculus globular, with tubular neck
 - B. Twelve longitudinal folds on intima, two ranks of 12 pyramidal teeth at posterior end; no prominent gastric caeca Grylloblattaria
 - BB. Six longitudinal folds on intima with series of sclerotized appendages; longitudinal folds separated by partitions; two bulbous gastric caeca lying lateral to proventriculus
 - C. Appendages with median tooth, median denticles, lateral teeth, lateral denticles, inner and outer barbed lobes Grylloidea
 - D. No posterior projection of median tooth; single median denticle or row of denticles Grylloptidae
 - DD. Posterior projection of median tooth with several median denticles Gryllidae
 - CC. Appendages with median tooth, lateral lobe, and single barbed lobe Tettigonioidea
 - D. Median tooth bearing a tuft of hairs; lateral lobes lightly sclerotized Rhaphidophoridae
 - DD. Median tooth without tuft of hairs; tooth heavily sclerotized Tettigoniidae, Stenopelmatidae, Prophalangopsidae
- AAA. Proventriculus tubular
 - B. No gastric caeca
 - C. Six longitudinal folds on intima, each with an anterior cushion of bristles Dermaptera
 - CC. Numerous longitudinal folds on intima Phasmida
 - BB. Two or six gastric caeca
 - C. Six longitudinal plates in the proventriculus; six gastric caeca, each with anterior and posterior projections Acrididae
 - CC. No longitudinal plates in proventriculus; gastric caeca with anterior projection only
 - D. Two gastric caeca Tridactylidae
 - DD. Six tubular gastric caeca Cylindrachetidae
 - DDD. Six conical gastric caeca Tetrigidae
 - BBB. Seven gastric caeca; 14 longitudinal plates in the proventriculus Plecoptera

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NOTE: *Figs. 1-98 will be found on pp. 143-161.*

EXPLANATION OF FIGURES

FIG. 1. *Parcoblatta pennsylvanica* DeGeer—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 2. *Mantis religiosa* Linnaeus—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 3. *Diapheromera femorata* Say—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 4. *Oecanthus nigricornis* Walker—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 5. *Neoconocephalus ensiger* Harris—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 6. *Ceuthophilus maculatus* Harris—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

C—*crop*; *GC*—*gastric caecum*; *MG*—*mid-gut*; *N*—*neck*; *P*—*proventriculus*.

FIG. 7. *Dissosteira carolina* Linnaeus—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 8. *Cylindrocytes spegazzinii* Giglio-Tos—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 9. *Tettigidea lateralis parvipennis* Harris—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 10. *Tridactylus apicalis* Say—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 11. *Grylloblatta campodeiformis* Walker—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 12. *Acroneuria abnormis* Newman—*proventriculus*, *posterior end of crop*, and *anterior end of mid-gut* (dorsal view).

C—*crop*; *GC*—*gastric caecum*; *MG*—*mid-gut*; *N*—*neck*; *P*—*proventriculus*.

FIG. 13. *Parcoblatta pennsylvanica* DeGeer—*sclerotized intima of proventriculus*.

FIG. 14. *Parcoblatta pennsylvanica* DeGeer—*longitudinal section of proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 15. *Parcoblatta pennsylvanica* DeGeer—*transverse section of proventriculus through anterior cushions*.

AC—*anterior cushion*; *CM*—*circular muscle*; *CT*—*sclerotized tooth*; *EP*—*epithelium*; *H*—*hairs*; *I*—*intima*; *LM*—*longitudinal muscle*; *MG*—*mid-gut*; *Oes. V.*—*oesophageal valve*; *PC*—*posterior cushion*; *PF*—*primary fold*; *RM*—*retractor muscle*; *S*—*large spine of sclerotized tooth*; *SF*—*secondary fold*; *Ss*—*small spine of sclerotized tooth*.

FIG. 16. *Pycnoscelus surinamensis* Linnaeus—*sclerotized intima of proventriculus*.

FIG. 17. *Blaberus atropos* Stoll—*sclerotized intima of proventriculus*.

AC—*anterior cushion*; *C*—*cushion*; *CT*—*sclerotized tooth*; *Oes. V.*—*oesophageal valve*; *OP*—*ovoid patch*; *P*—*patch covered with bristles*; *PC*—*posterior cushion*; *PF*—*primary fold*.

FIG. 18. *Periplaneta americana* Linnaeus—*sclerotized intima of proventriculus*: *teeth (CT) numbered from left to right, 1, 2, 3, 4, 5, 6*.

FIG. 19. *Cryptocercus punctulatus* Scudder—*sclerotized intima of proventriculus*.

AC—*anterior cushion*; *AS*—*anterior spine of anterior cushion*; *CT*—*sclerotized tooth*; *Oes. V.*—*oesophageal valve*; *PC*—*posterior cushion*; *PF*—*primary fold*; *PS*—*posterior spine of anterior cushion*; *SC*—*secondary cushion*; *SF*—*secondary fold*.

FIG. 20. *Mantis religiosa* Linnaeus—*sclerotized intima of proventriculus showing form of the six teeth*.

FIG. 21. *Mantis religiosa* Linnaeus—*transverse section through teeth*.

FIG. 22. *Mantis religiosa* Linnaeus—*transverse section through anastomosing ridges*.

FIG. 23. *Mantis religiosa* Linnaeus—*transverse section through anterior cushions*.

AC—*anterior cushion*; *AR*—*anastomosing ridges*; *CC*—*cushion of hairs*; *CH*—*hairs*; *CM*—*circular muscle*; *CT*—*sclerotized tooth*; *EP*—*epithelium*; *FT*—*forked tip*; *I*—*intima*; *LM*—*longitudinal muscle*; *Oes. V.*—*oesophageal valve*; *PC*—*posterior cushion*; *R*—*ridge*.

FIG. 24. *Diapheromera femorata* Say—*longitudinal section through proventriculus*, *posterior end of crop*, and *anterior end of mid-gut*.

FIG. 25. *Diapheromera femorata* Say—*sclerotized intima of crop and proventriculus*.

FIG. 26. *Diapheromera femorata* Say—*longitudinal folds of crop*.

FIG. 27. *Anisomorpha buprestoides* Stoll—*longitudinal folds of crop*.

FIG. 28. *Hadenoecus puteanus* Scudder—*sclerotized intima of one longitudinal fold of proventriculus*.

BL—*barbed lobe*; *C*—*crop*; *CC*—*cushion of hairs*; *CM*—*circular muscle*; *CP*—*sclerotized partition*; *CT*—*sclerotized tooth*; *EP*—*epithelium*; *FL*—*flap of oesophageal valve*; *I*—*intima*; *Inv.*—*invagination into proventriculus*; *LF*—*longitudinal fold*; *LL*—*lateral lobe*; *LM*—*longitudinal muscle*; *MG*—*mid-gut*; *MT*—*median tooth*; *Oes. V.*—*oesophageal valve*; *P*—*proventriculus*; *S*—*spine*.

FIG. 29. *Oecanthus nigricornis* Walker—*transverse section through median tooth of sclerotized appendage*.

FIG. 30. *Oecanthus nigricornis* Walker—*transverse section through median denticles of sclerotized appendage*.

FIG. 31. *Oecanthus nigricornis* Walker—*transverse section through lateral teeth of sclerotized appendage*.

FIG. 32. *Oecanthus nigricornis* Walker—*two longitudinal folds of intima of neck and body of proventriculus*.

FIG. 33. *Falcicula hebardi* Rehn—*sclerotized intima of proventriculus*.

FIG. 34. *Phyllopalpus pulchellus* Uhler—sclerotized appendage of proventriculus.

FIG. 35. *Cyrtoxipha columbiana* Caudell—sclerotized appendage of proventriculus.

CA—sclerotized appendage; CL—sclerotized lobe; CM—circular muscle; CP—sclerotized partition; EP—epithelium; I—intima; IBL—inner barbated lobe; LD—lateral denticle; LM—longitudinal muscle; LT—lateral tooth; MD—median denticle; MT—median tooth; OBL—outer barbated lobe; Oes. V.—oesophageal valve.

FIG. 36. *Gryllulus assimilis* Fabricius—longitudinal section of proventriculus.

FIG. 37. *Scapteriscus vicinus* Scudder—sclerotized appendage of proventriculus.

FIG. 38. *Nemobius fasciatus* DeGeer—sclerotized appendage of proventriculus.

FIG. 39. *Gryllulus domesticus* Linnaeus—sclerotized appendage of proventriculus.

FIG. 40. *Oecanthus nigricornis* Walker—sclerotized appendage of proventriculus.

FIG. 41. *Scapteriscus vicinus* Scudder—sclerotized intima of one longitudinal fold.

FIG. 42. *Hapithus brevipennis* Saussure—sclerotized appendage of proventriculus.

FIG. 43. *Tafalisca lurida* Walker—sclerotized appendage of proventriculus.

CC—cushion of hairs; CM—circular muscle; CP—sclerotized partition; EP—epithelium; GC—gastric caecum; I—intima; IBL—inner barbated lobe; LD—lateral denticle; LM—longitudinal muscle; LT—lateral tooth; MD—median denticle; MT—median tooth; N—neck of proventriculus; OBL—outer barbated lobe; Oes. V.—oesophageal valve; T—sclerotized appendage.

FIG. 44. *Cycloptilum squamosum* Scudder—sclerotized intima of one longitudinal fold of proventriculus.

FIG. 45. *Myrmecophila oregonensis* Brunner—sclerotized intima of one longitudinal fold of proventriculus.

FIG. 46. *Gryllotalpa hexadactyla* Perty—sclerotized appendage of proventriculus.

FIG. 47. *Anurogryllus muticus* DeGeer—sclerotized appendage of proventriculus.

FIG. 48. *Neoconocephalus ensiger* Harris—sclerotized intima of two longitudinal folds of the proventriculus.

BL—barbated lobe; C—cushion of hairs; CH—loop of hairs; CP—sclerotized partition; CT—sclerotized tooth; IBL—inner barbated lobe; LD—lateral denticle; LL—lateral lobe; LT—lateral tooth; MD—median denticle; MT—median tooth; OBL—outer barbated lobe; Oes. V.—oesophageal valve; T—sclerotized appendage.

FIG. 49. *Neoconocephalus ensiger* Harris—transverse section of proventriculus, through sclerotized appendages.

FIG. 50. *Conocephalus fasciatus* DeGeer—sclerotized intima of two longitudinal folds of proventriculus.

FIG. 51. *Conocephalus fasciatus* DeGeer—transverse section through neck of proventriculus.

FIG. 52. *Conocephalus fasciatus* DeGeer—transverse section through oesophageal valve.

FIG. 53. *Conocephalus fasciatus* DeGeer—transverse section through sclerotized appendage.

BL—barbated lobe; C—cushion of hairs; CH—loop of hairs; CM—circular muscle; CP—sclerotized partition; CT—sclerotized tooth; EP—epithelium; I—intima; LL—lateral lobe; LM—longitudinal muscle; MT—median tooth; Oes. V.—oesophageal valve; T—sclerotized appendage.

FIG. 54. *Atlanticus gibbosus* Scudder—sclerotized intima of one longitudinal fold of proventriculus.

FIG. 55. *Atlanticus gibbosus* Scudder—sclerotized appendage of proventriculus.

FIG. 56. *Pholidoptera griseoaptera* DeGeer—sclerotized appendage of proventriculus.

FIG. 57. *Chelidoptera albopunctata* Goeze—sclerotized appendage of proventriculus.

FIG. 58. *Neduba carinata* Walker—sclerotized appendage of proventriculus.

FIG. 59. *Anabrus simplex* Haldemann—sclerotized appendage of proventriculus.

FIG. 60. *Pediocetes haldemanni* Girard—sclerotized appendage of proventriculus.

FIG. 61. *Stenopelmatus fuscus* Haldemann—sclerotized appendage of proventriculus.

FIG. 62. *Hemideina megacephala* Buller—sclerotized appendage of proventriculus.

FIG. 63. *Cratomelus* sp.—sclerotized appendage of proventriculus.

FIG. 64. *Hadenoecus puteanus* Scudder—sclerotized appendage of proventriculus.

FIG. 65. *Tachycines asynamorus* Adelung—sclerotized appendage of proventriculus.

BL—barbated lobe; C—cushion of hairs; CH—loop of hairs; CP—sclerotized partition; CT—sclerotized tooth; LL—lateral lobe; LP—lateral projection; MT—median tooth; Oes. V.—oesophageal valve.

FIG. 66. *Ceuthophilus maculatus* Harris—sclerotized intima of proventriculus.

FIG. 67. *Scudderia curvicauda* DeGeer—transverse section through neck of proventriculus.

FIG. 68. *Scudderia curvicauda* DeGeer—transverse section through a sclerotized appendage of proventriculus.

FIG. 69. *Scudderia curvicauda* DeGeer—sclerotized intima of one longitudinal fold of proventriculus.

BL—barbed lobe; CC—cushion of hairs; CH—hairs; CM—circular muscle; CP—sclerotized partition; CS—sclerotized spines; CT—sclerotized tooth; EP—epithelium; I—intima; MT—median tooth; Oes. V.—oesophageal valve.

FIG. 70. *Dissosteira carolina* Linnaeus—sclerotized intima of proventriculus and posterior end of crop.

FIG. 71. *Dendrotettix quercus* Packard—sclerotized intima of proventriculus and posterior end of crop.

FIG. 72. *Chloea altis conspersa* Harris—sclerotized intima of proventriculus and posterior end of crop.

FIG. 73. *Cyphoderris monstrosa* Uhler—sclerotized appendage of proventriculus.

FIG. 74. *Cyphoderris monstrosa* Uhler—sclerotized appendage of proventriculus, lateral view.

LL—lateral lobe; LP—longitudinal plate of proventriculus; LR—longitudinal ridge of crop; MT—median tooth; S—scalelike spine of crop.

FIG. 75. *Dissosteira carolina* Linnaeus—transverse section of crop.

FIG. 76. *Dissosteira carolina* Linnaeus—transverse section of crop anterior to proventricular plates.

FIG. 77. *Dissosteira carolina* Linnaeus—transverse section of proventriculus through anterior ends of proventricular plates.

FIG. 78. *Dissosteira carolina* Linnaeus—transverse section of proventriculus through posterior end of proventricular plates.

FIG. 79. *Tettigidea lateralis parvipennis* Harris—longitudinal section of proventriculus, posterior end of crop, and of anterior end of mid-gut.

FIG. 80. *Paratettix cucullatus* Burmeister—sclerotized intima of proventriculus and posterior end of crop.

FIG. 81. *Cylindrorcytes spegazzini* Giglio-Tos—sclerotized intima of proventriculus and posterior end of crop.

FIG. 82. *Tridactylus apicalis* Say—sclerotized intima of proventriculus and crop.

C—crop; CM—circular muscle; EP—epithelium; GC—gastric caecum; H—head; I—intima; LF—longitudinal fold of proventriculus; LM—longitudinal muscle; LR—longitudinal ridge of crop; MG—mid-gut; Oes. V.—oesophageal valve; P—proventriculus; TM—transverse muscle.

FIG. 83. *Tridactylus apicalis* Say—transverse section of proventriculus and gastric caeca.

FIG. 84. *Termopsis angusticollis* Hagen—sclerotized intima of proventriculus.

C—cushion; CM—circular muscle; CT—sclerotized tooth; EP—epithelial layer; GC—gastric caecum; I—intima; LF—longitudinal fold; Oes. V.—oesophageal valve.

FIG. 85. *Grylloblatta campodeiformis* Walker—sclerotized intima of proventriculus.

FIG. 86. *Grylloblatta campodeiformis* Walker—transverse section through primary folds of proventriculus.

FIG. 87. *Grylloblatta campodeiformis* Walker—transverse section through primary and secondary folds of proventriculus.

FIG. 88. *Grylloblatta campodeiformis* Walker—longitudinal section through proventriculus and anterior end of mid-gut.

CM—circular muscle; EP—epithelium; GC—gastric caecum; I—intima; LM—longitudinal muscle; N—neck of proventriculus; Oes. V.—oesophageal valve; PF—primary fold; PT1—pyramidal tooth (first row); PT2—pyramidal tooth (second row); S—scalelike spines; SF—secondary fold.

FIG. 89. *Grylloblatta campodeiformis* Walker—transverse section through primary and secondary pyramidal teeth of proventriculus.

FIG. 90. *Grylloblatta campodeiformis* Walker—transverse section through one primary and two secondary pyramidal teeth of proventriculus.

FIG. 91. *Grylloblatta campodeiformis* Walker—transverse section through secondary pyramidal teeth of proventriculus.

FIG. 92. *Grylloblatta campodeiformis* Walker—transverse section through one secondary pyramidal tooth of *proventriculus*.

FIG. 93. *Acroneuria abnormis* Newman—longitudinal plate of *proventriculus*.

FIG. 94. *Acroneuria abnormis* Newman—sclerotized intima of *proventriculus*.

CH—hairs; CM—circular muscle; EP—epithelium; I—intima; LM—longitudinal muscle; LT—longitudinal plate; PT1—pyramidal tooth (first row); PT2—pyramidal tooth (second row).

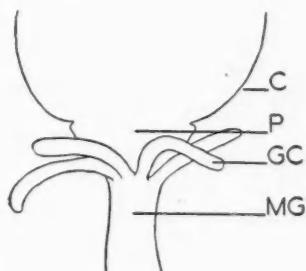
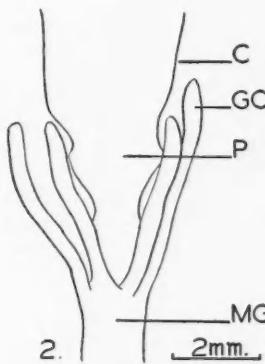
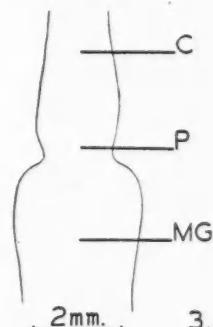
FIG. 95. *Acroneuria abnormis* Newman—transverse section through posterior end of longitudinal plates of *proventriculus*.

FIG. 96. *Acroneuria abnormis* Newman—transverse section through posterior end of *proventriculus*.

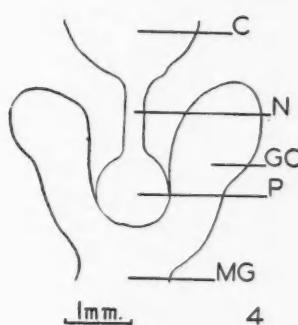
FIG. 97. *Anisolabis maritima* Boller—*proventriculus*, posterior end of *crop*, and anterior end of *mid-gut*.

FIG. 98. *Anisolabis maritima* Boller—sclerotized intima of *proventriculus*.

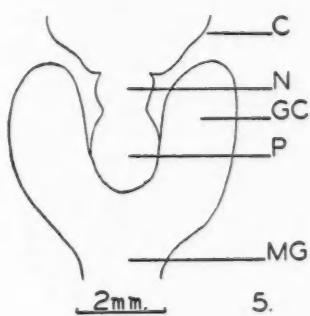
C—*crop*; CC—cushion of hairs; CM—circular muscle; EP—epithelium; LF—longitudinal fold; LM—longitudinal muscle; LT—longitudinal plate; MG—*mid-gut*; Oes. V.—oesophageal valve; P—*proventriculus*.

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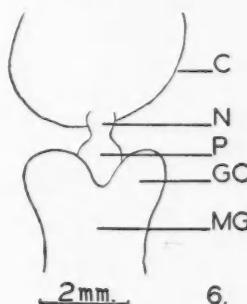
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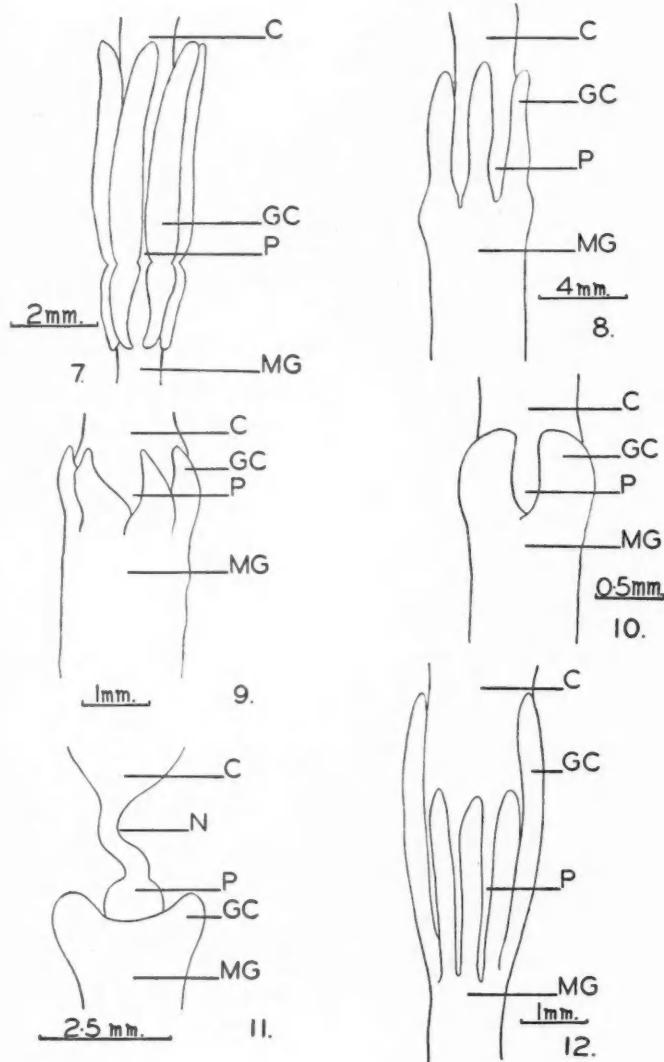
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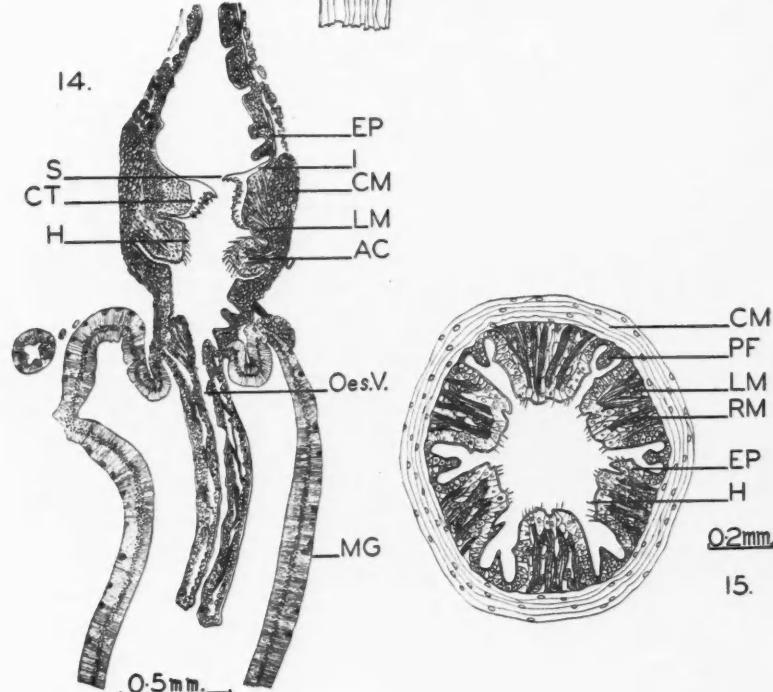
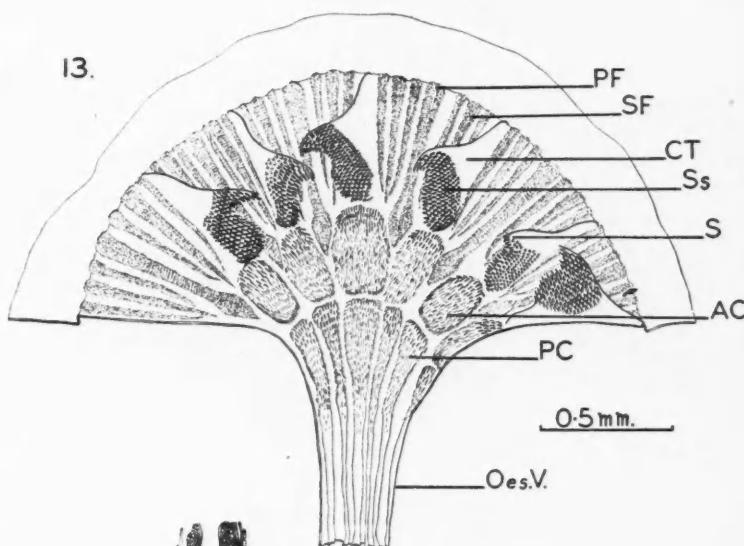


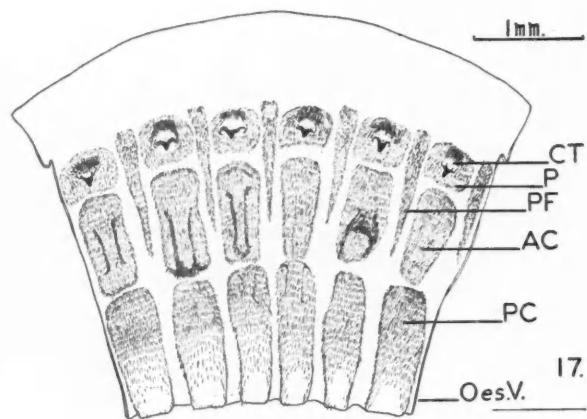
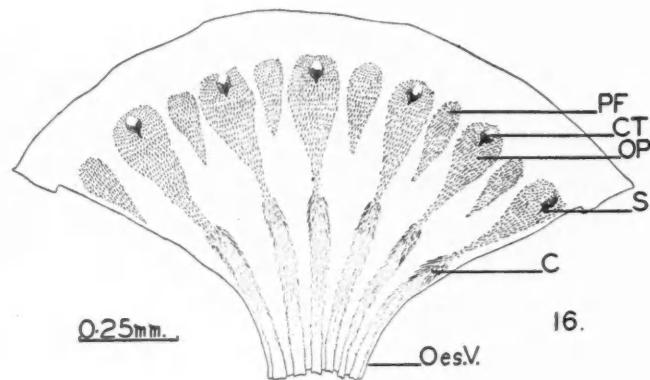
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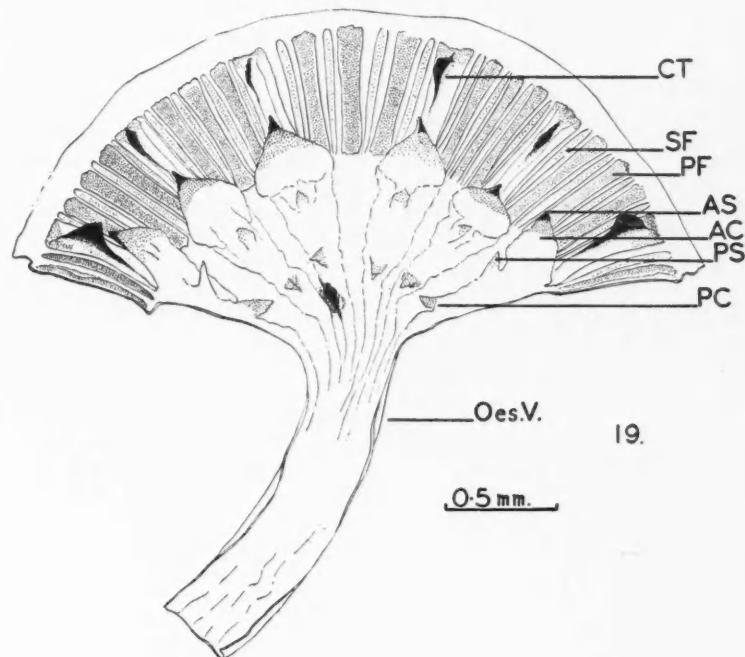
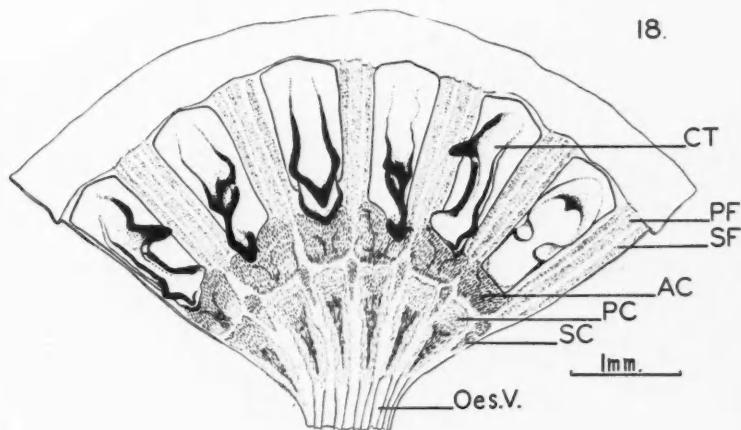


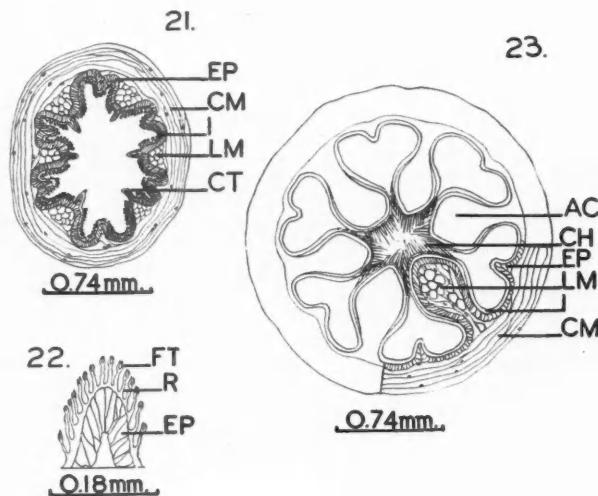
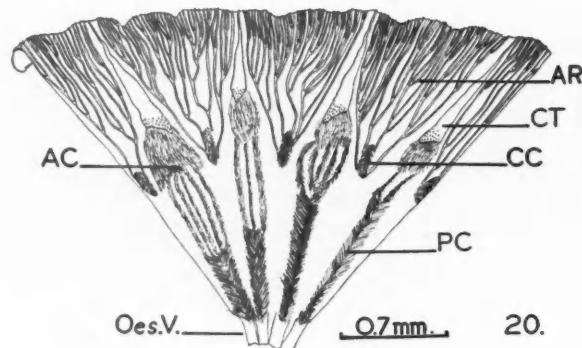
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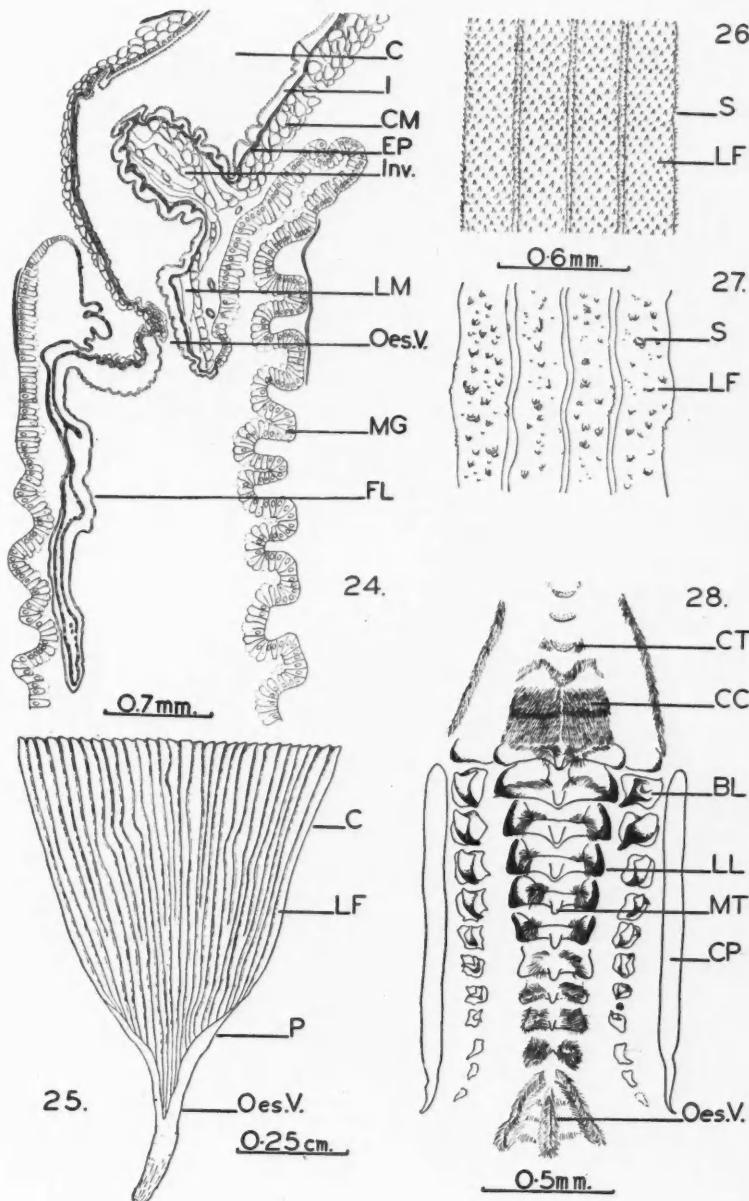


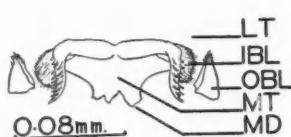
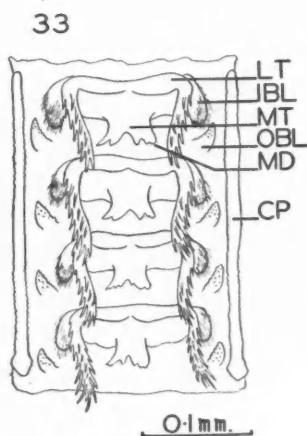
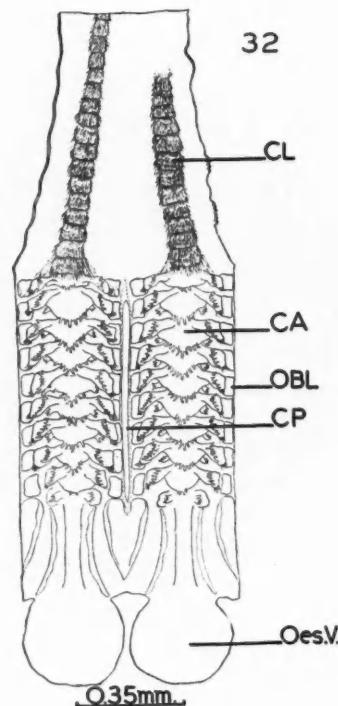
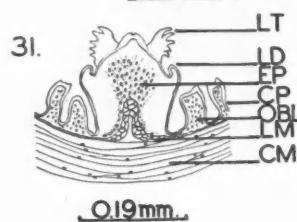
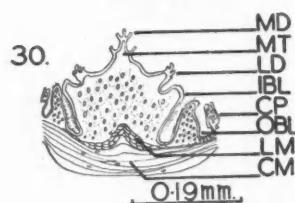
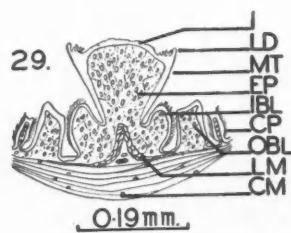


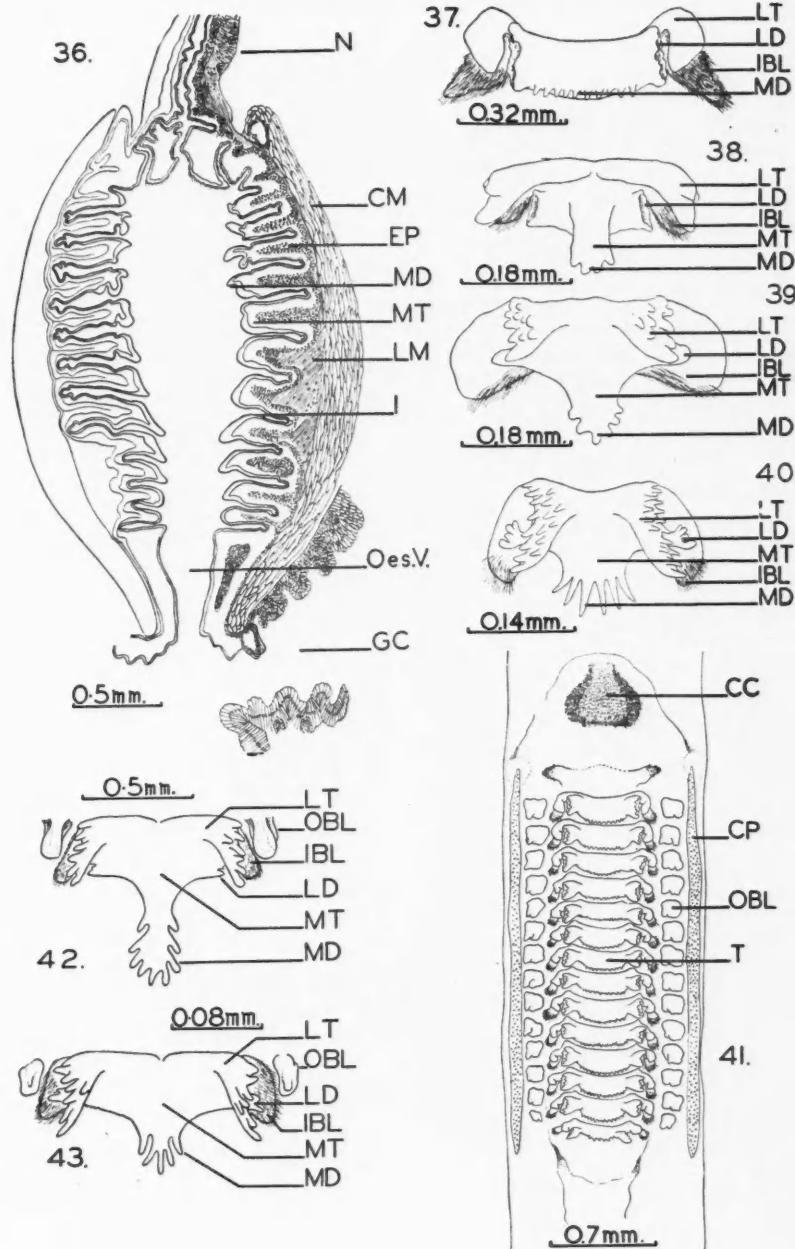


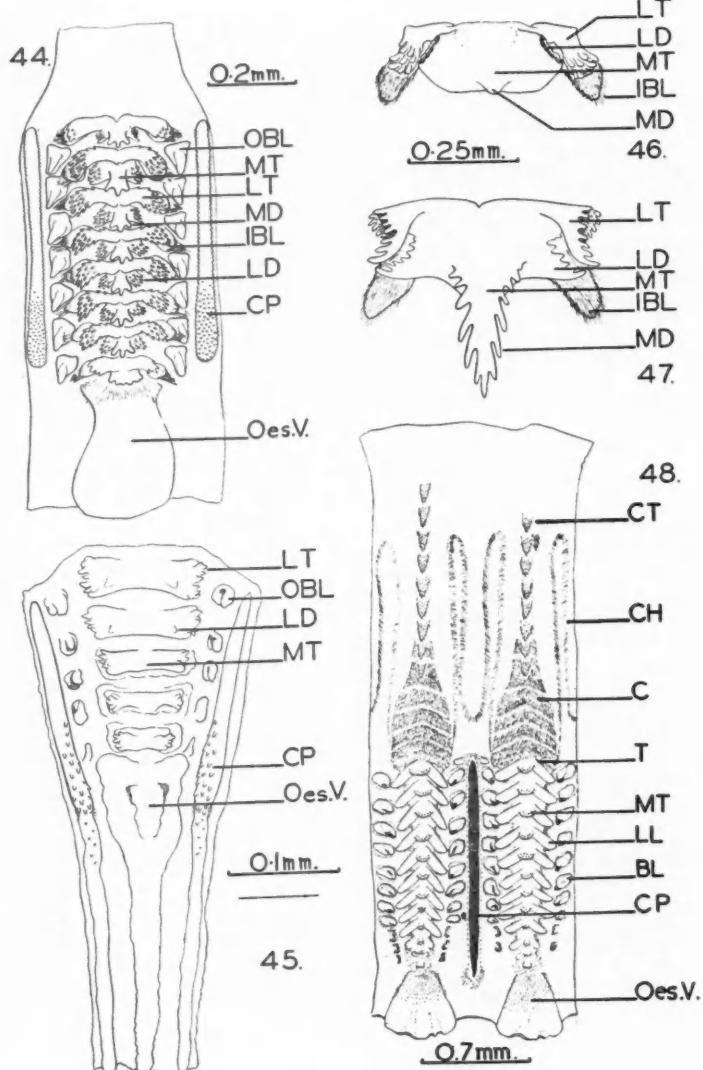




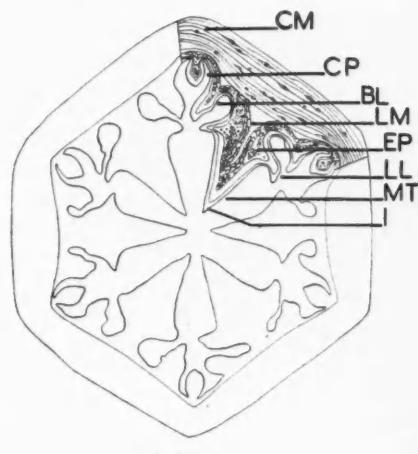






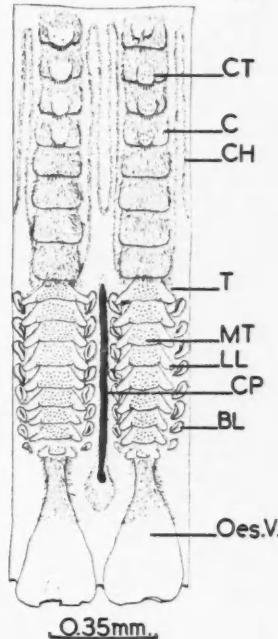


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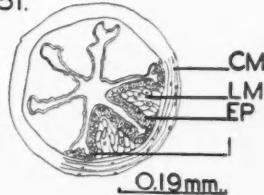
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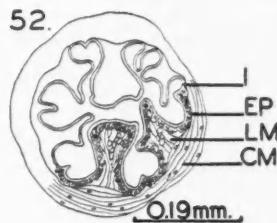
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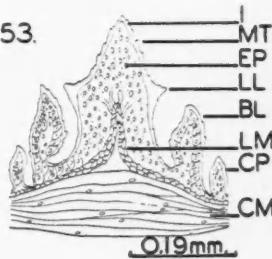
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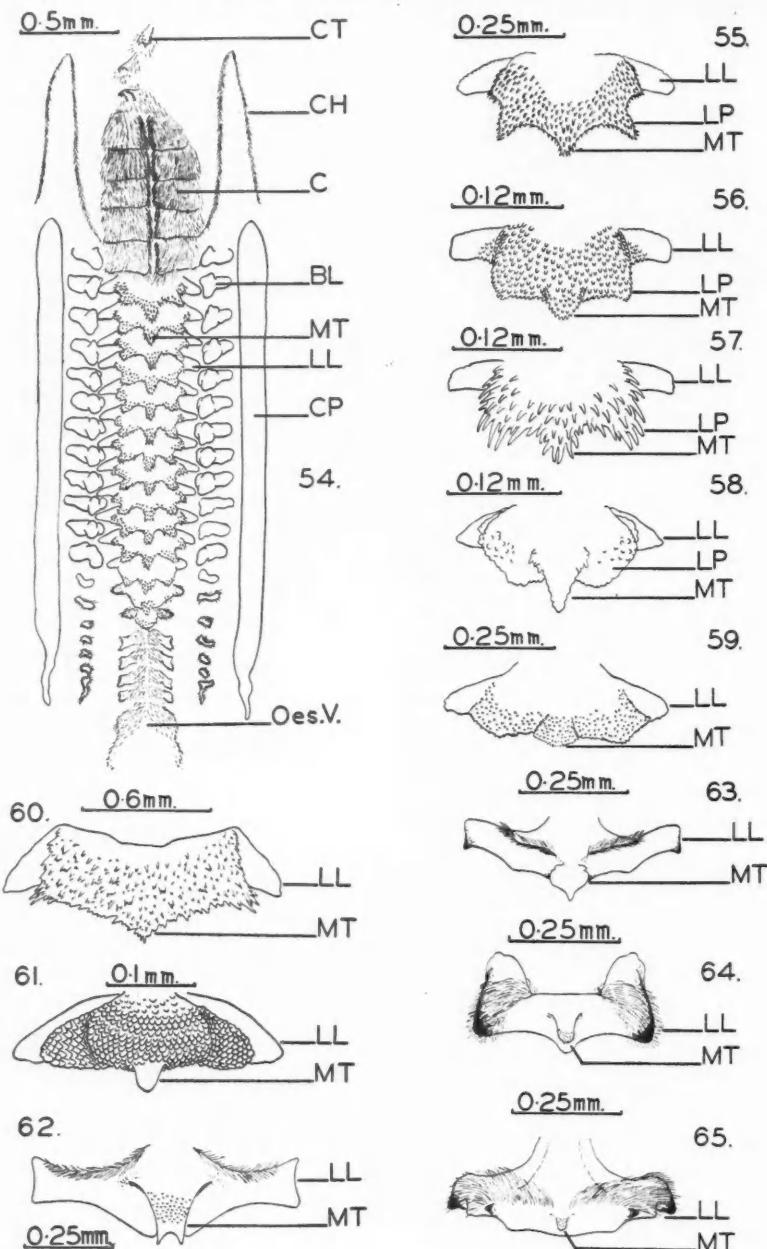


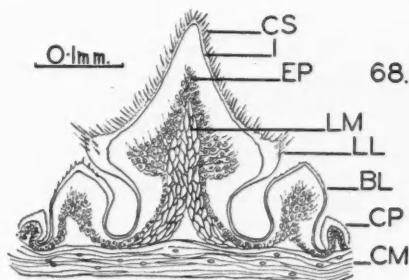
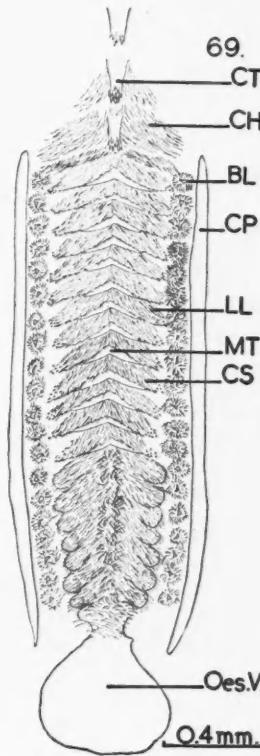
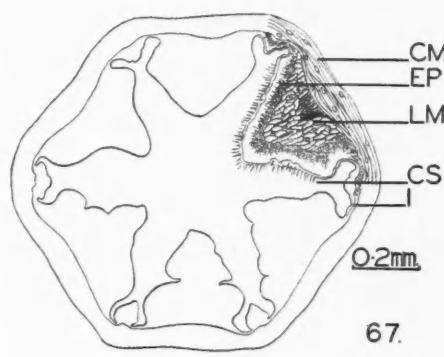
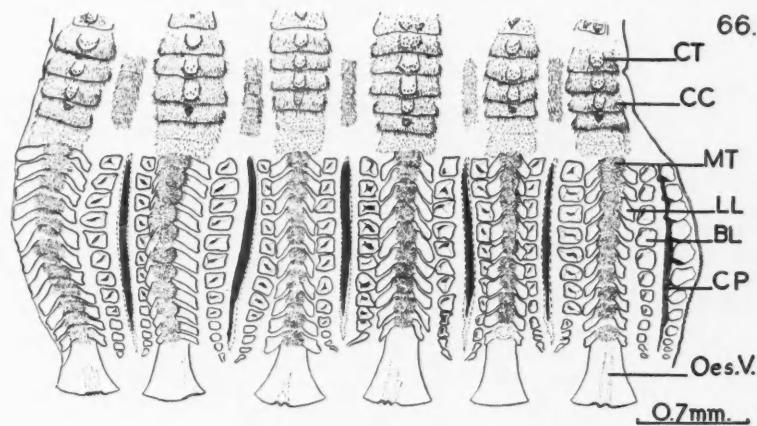
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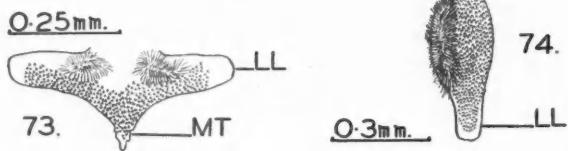
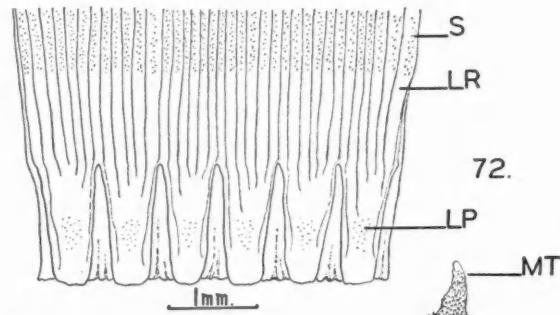
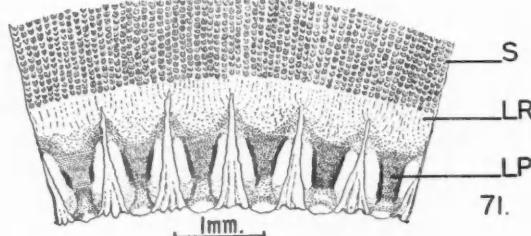
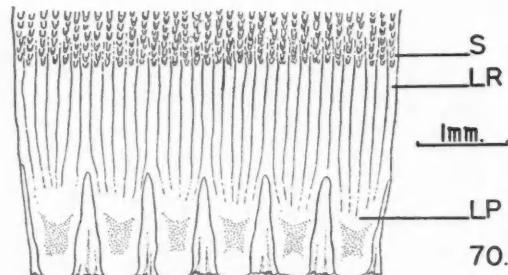
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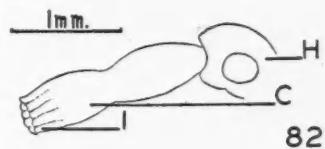
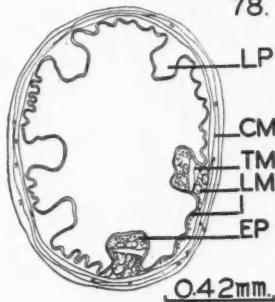
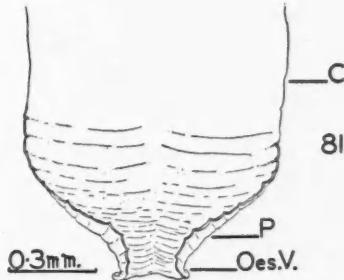
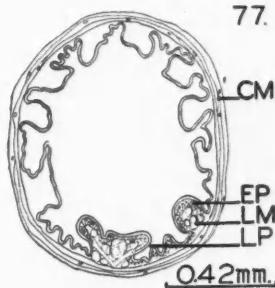
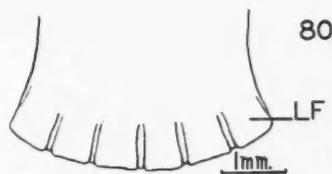
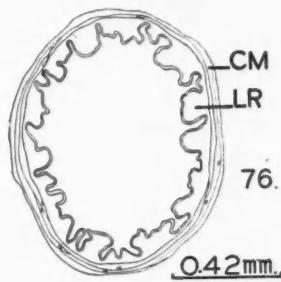
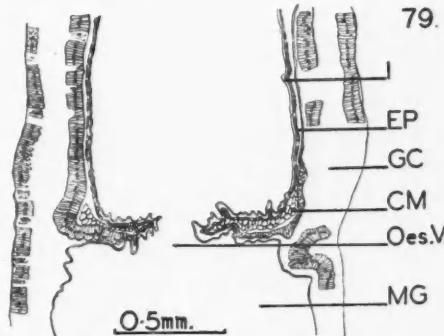
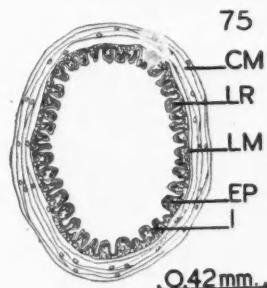


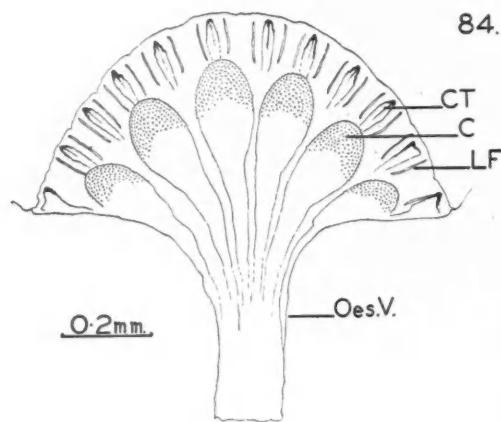
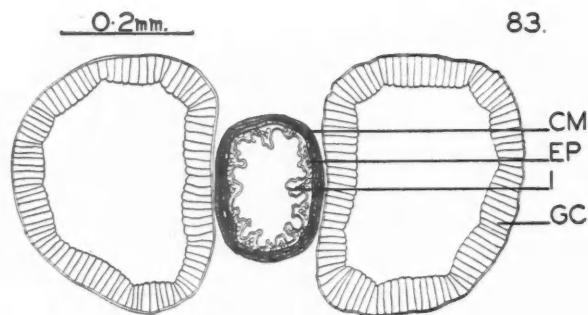
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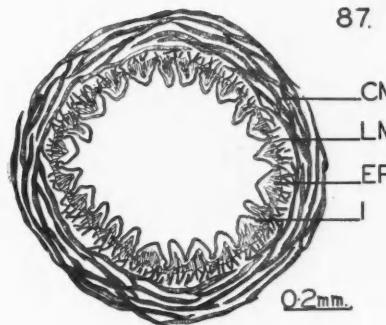
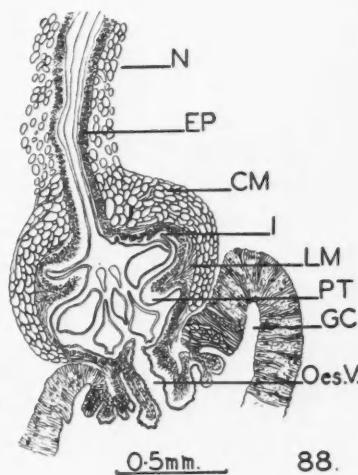
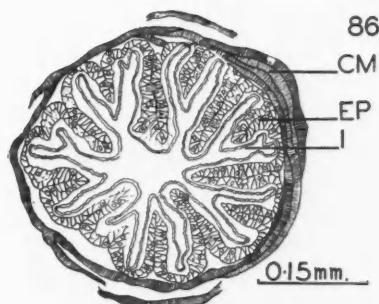
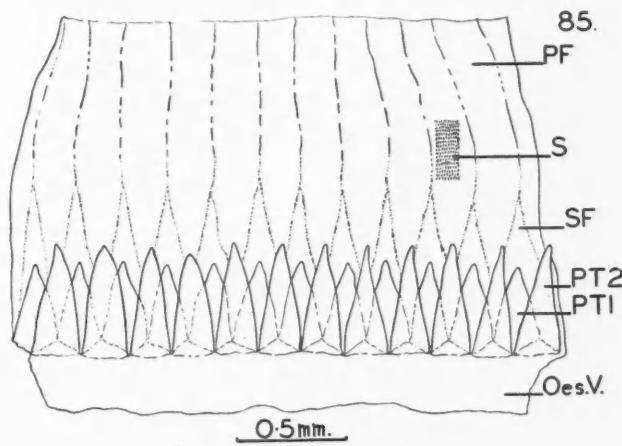




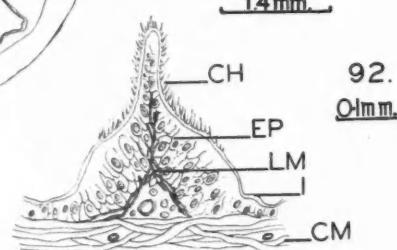
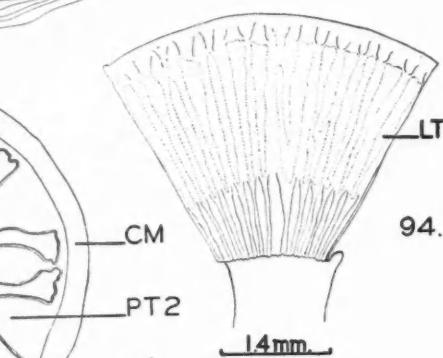
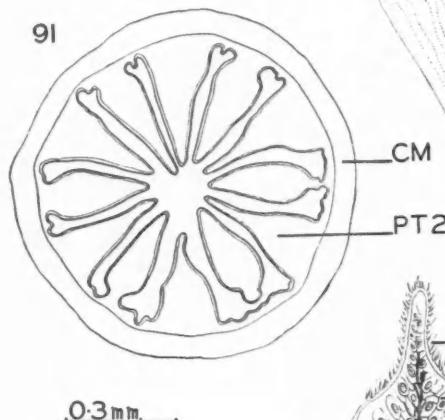
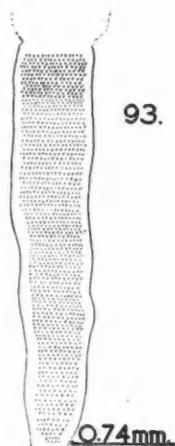
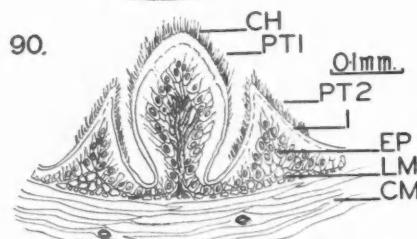
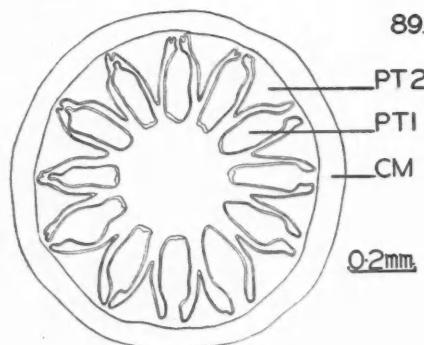


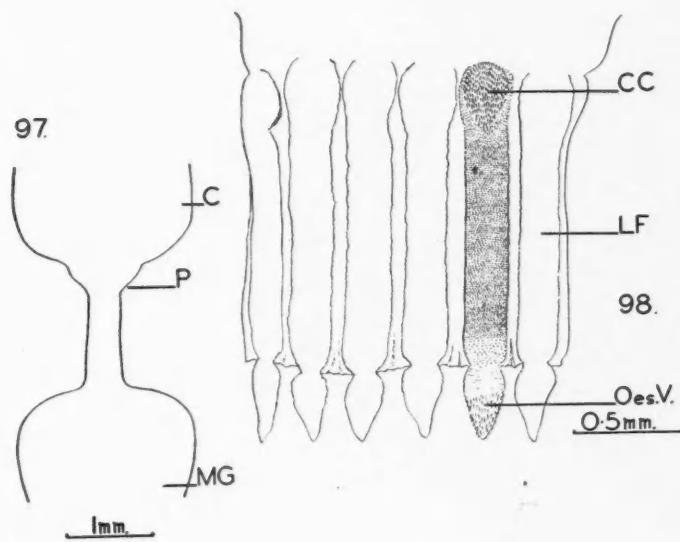
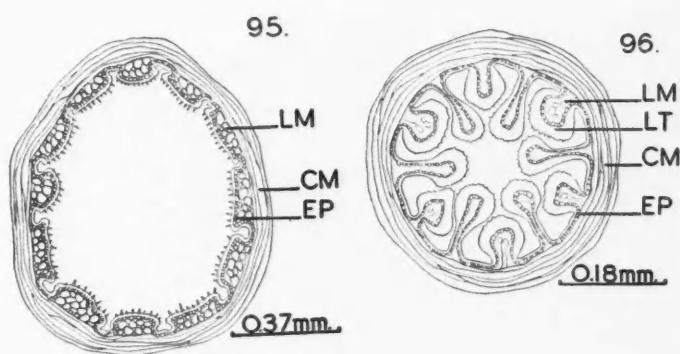






88.





CANADIAN JOURNAL OF RESEARCH

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